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First Year Sprouting and Growth Dynamics of Northern Red Oak, Yellow-Poplar, Red Maple, and Sweet Birch on a Mesic Site Following a Release Burn During a "Shelterwood-Burn" Sequence.

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Abstract

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Maria Adele Fenwick

Oak regeneration challenges are a widespread issue across the mixed oak and mixed mesophytic forests of the eastern United States. Following disturbance on many mesic and sub-mesic sites oaks are being replaced by faster growing or shade tolerant species. There are many contributing factors, but one thought to have the strongest influence is attributed to the effects of 20th century fire suppression. For millennia fire was an integral part of oak dominated ecosystems and is thought to have contributed to and perpetuated oak's importance in these forests. During the 20th century the frequency and spatial scale of fire was severely reduced in most eastern forests. In the absence of fire, oaks are unable to benefit from their unique developmental and physiological traits superiorly adapted to a periodic fire regime and maintain their dominance. The fire adapted traits important at different life stages of oaks include modest growing site requirements, hypogeal germination, early growth strategy of root development over of shoot development, ability to repeatedly sprout following dieback or topkill, development of thick fire resistant bark, and ability to compartmentalize wounds. As the ecological effects of fire suppression have materialized and compounded over time, prescribed fire has emerged as a silvicultural tool to modify competitive dynamics in an effort to maintain or restore oak communities. Although there are a rapidly increasing number of prescribed fire studies, replications are still necessary with different combinations of variables to determine the conditions that will produce successful results with greater certainty. This goal of this study was to examine the competitive relationship between oak seedlings and three of its competitors, develop first year survival probability models, and assess post-fire sprout growth dynamics. First year data show that oak survived at a higher rate than red maple, sweet birch, and yellow-poplar, and the differences were more apparent at smaller sizes. Probability of survival models as a function of height are superior to survival models as a function of diameter for red maple, sweet birch, and yellow-poplar. Oak survival was so high a meaningful survival probability model could not be developed.

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INTRODUCTION

Boundaries and definitions vary, but the central hardwood region is a vast forested area of about 235,000 square miles that is generally centered along the axes of the Appalachian Mountains from New York to Georgia and to the Ozark/Ouachita Mountains in Missouri and Arkansas (Hicks 1998). Eighteen oak species that dominate stands unify the region, and species such as white (*Quercus alba*), black (*Q. velutina*), and chestnut oak (*Q. prinus*) may form mature communities on xeric sites or successional communities on mesic sites (Fralish 2003). The oak-dominated central hardwood forests have a developmental history shaped by myriad ecological and anthropogenic influences and disturbance regimes. Fire, perhaps more than any single factor, has been implicated in the expansion, perpetuation, and decline of oak communities, and the effects of fire prevention and suppression since the turn of the century have had a dramatic influence on the ecological dynamics and succession of oak the forests that we see today (Hicks 1998).

As a stand matures and overstory oaks grow in size, oak basal area per acre may increase but frequently it represents a decreasing proportion of the total basal area in the stand (Moser et al. 2006). As overstory trees are harvested or experience natural mortality, decline in oak abundance is being witnessed, which can be attributed to either there being insufficient oak regeneration, or the regeneration present was not competitive enough to be recruited into the overstory as stands develop (Smith, D.W. 1993). Despite mitigation efforts, a decline in oak abundance is occurring in stands subjected to various management techniques as well as in unmanaged stands (Schuler and Miller 1995). Declines are not geographically universal, but have been especially severe in the Allegheny/Appalachian plateaus in the central hardwood region (Fei et al. 2011).

Compositional shifts are more pronounced on mesic sites where oaks are being replaced by fire-sensitive species that are thriving in the absence of fire, including those that are shade tolerant and present in the understory at the time of disturbance, as well as those that are able to more rapidly respond to the disturbance. On more xeric sites, species replacing oak typically include those that more shade tolerant and have accumulated in the understory (Johnson et al. 2009, Lorimer 1993). Species vary by region but shade tolerant species on mesic sites may include maples (*Ace*r spp.), American beech (*Fagus grandifolia*), and blackgum (*Nyssa sylvatica*). Fast growing species may include yellow-poplar (*Liriodendron tulipifera*), black cherry (*Prunus serotina*) and sweet birch (*Betula lenta*) (Crow 1998, Lorimer 1984, Schuler and Gillespie 2000, Schuler 2004, Trimble 1970). This conversion process has been termed by Nowacki and Abrams (2008) as “mesophication”, and is attributed to, and perpetuated by, a change in disturbance regimes, specifically the absence of periodic fire for much of the 20th century. Other than fire, no other form of natural disturbance discriminates against maple, beech, and other typical understory competitors, to favor oak (Rentch et al. 2003).

It is established that oak is a fire-adapted species and both its distribution and dominance was likely in large part supported and sustained by a recurrent fire regime, as indicated by numerous types of historical records and studies (Abrams 1992, Yaussy 2000). Efforts to restore and maintain oak communities are being undertaken with an adaptive management approach and unified monitoring system (Gottschalk et al. 2014, Nowacki et al. 2009, Yaussy et al. 2008).

Silvicultural guidelines developed to sustain oak include various harvest techniques and sequences, artificial regeneration with plantings, herbicide applications, and fencing (Brose et al. 2008, Johnson et al. 2009, Loftis 1990b, Steiner et al. 2008). Prescribed fire has evolved from being a speculative proposition (Little 1973), to now being established as an effective component of silvicultural treatments in certain situations to mitigate the declining importance value of oak (Brose 2014). Importance value is an index of frequency, density, and dominance of a species in a stand (Fei et al. 2011). Fire is not a panacea and prudence is necessary when prescribing burn treatments, as there are certain parameters necessary to create conditions for success in promoting oak and deviation from these parameters can lead to results that are ambiguous or detrimental to oak (Brose et al. 2013).

Departure from the historic fire regime has altered canopy accession pathways and shifted understory species composition (Rentch et al. 2003). Both of these factors have resulted in increased forest density and understory shade, precipitating the rise in shade tolerant species, particularly red maple (*Acer rubrum*), and perpetuating their presence (Lorimer 1984). Partial harvesting and uneven-age management schemes that typically decrease light levels penetrating the canopy are associated with the decline of oaks because the functionality of past recruitment mechanisms has changed (Schuler 2014).

Significant advancements have been made in identifying the conditions that are most likely to benefit oak communities, but there is still a need for additional information regarding the impact of fire on seedling sprouting, survival, and growth in mesic forests of the central Appalachians (Schuler, T.M. et al. 2013). The study discussed herein is part of a more comprehensive examination of the efficacy of prescribed fire using the “shelterwood-burn technique” (Brose et al. 1999b) to regenerate oak on two mesic mixed-oak sites the Fernow Experimental Forest in West Virginia. Benefits of prescribed fire proposed in the shelterwood-burn sequence include facilitating oak seedling establishment and release from competition to promote successful overstory recruitment.

Topics including why oak ecosystems are important, their developmental history and successional pathways, the role of fire in oak maintenance and restoration, and silvicultural management implications will be discussed herein.

IMPORTANCE OF OAK ECOSYSTEMS

Economic Value

The central hardwood region is one of the largest, if not the largest area of deciduous hardwoods in the world and contains a mixture of economically valuable tree species (Hicks 1998). Although consumer tastes and preferences change through time, oak has historically maintained its presence among the most valuable hardwoods shown in the Hardwood Market Statistics Bulletin (Jones 2013). The forestry and logging, paper and wood product manufacturing, forestry support sectors, and associated markets are dependent on harvest volume and quality. The strength of domestic and export market is dependent on the ability to meet the demand for oak. Also of economic value are various other ecosystem services and amenities forests provide in the age of multiple-use management including carbon sequestration, landscape aesthetics, and recreation.

Wildlife Habitat

Many mammals and birds are dependent on acorns and it is important to maintain the mast-producing capability of the forest with both red and white oak group (*Quercus* section *Lobate* and *Quercus* section *Quercus*) species (McShea and Healy 2002). Wildlife are highly dependent on oak species since the demise of American chestnut (*Castanea dentata*) and spread of beech bark disease (*Nectria coccinea*) have reduced hard mast sources. During the winter when options are scarce, acorns provide one of the only food sources.

The longevity of oaks creates stable plant communities (Smith 2006) which provides the long-term contribution of hard mast and unique habitat conditions. These conditions provide habitat for species dependent on tree height or diameter for den or nest sites, particular bark texture, or canopy or understory structure. For example, endangered Indiana bats show an affinity for large roost trees with exfoliating bark, highlighting the importance of retaining potential day-roost trees near hibernaculum sites (Ford et al. 2002). There is positive association between floristic structural diversity and avifaunal diversity, and conservation efforts have been focused on the effects of different silvicultural practices following songbird population declines in many eastern forests (Lanham et al. 2006). Neotropical migratory songbirds such as the Cerulean warbler depend on habitat provided by oak dominated stands that have large diameter trees and relatively open upper canopies (Wood et al. 2013).

Wildlife are also dependent on oak foliage as a source for browse. Fire affects habitat by enhancing palatability and increasing nutrient content in post-burn growth, and making more sources reachable from those sprouting on the forest floor (Van Lear and Harlow 2002).

Wildlife population dynamics and health are influenced by food sources, habitat condition and size, and the evolution of hunting and wildlife management practices and policies. Fire did not burn uniformly across the landscape, but interacted with topographic, edaphic, vegetative, and weather conditions to produce a mosaic of habitat types and ecotones (McShea and Healy 2002). Fire suppression in the last 100 years has resulted in a dramatic decline in fire-maintained habitats, resulting in the decline or low populations of wildlife species dependent on these habitats (Van Lear and Harlow 2002). Both of these factors stress the need to develop effective methods to retain oak.

Biodiversity and Ecosystem Function

Because of their cascading influences on ecosystem processes, community dynamics, and biodiversity, oaks play a keystone role in ecosystem function (Fralish 2004). Dynamics and biodiversity include that of forest canopy composition, understory plant communities supported by oak canopy structure and light levels, and wildlife species.

High biodiversity enables a forest to respond to and recover from external influences and disturbances. Furthermore, biodiversity provides the ability to be resilient while still maintaining essential ecosystem processes such as regeneration, nutrient cycling, sustaining wildlife, and supporting air and water quality (Johnson et al. 2009). Forests are continuously subject to pressures of varying types and scales including invasive insect, pathogen, and plant species, climatic factors, disturbances, and land use changes.

The species that have increased in importance as oak has decreased, such as maples, American beech, yellow-poplar, and sweet birch, do not have comparable ecological or economic value to oak (Gribko et al. 2002). Economic stability of the forest products industry, supporting wildlife populations, and maintaining forest health and ecosystem function highlights the urgency of identifying a sustainable way to maintain oak dominated communities. The sustainability of oak communities under current disturbance regimes is questionable, which foreshadows a future forest composition with a smaller proportion of oak in the overstory and thus a reduction of the many benefits that oak forests provide.

FACTORS IN THE DEVELOPMENT OF EASTERN OAK FORESTS

The legacy of oak dominance is largely attributable to their ability to prosper during periods of disturbance and environmental stress (Hicks 1998). A common denominator in the disturbance history spanning the duration and expansion of oaks across eastern forests is the frequent fire return interval. In the Appalachians, it is estimated that the mean fire interval (MFI) was 5.8 years before European settlement, 5.3 years after European settlement, and has risen to 32.4 years since the beginning of forest fire control policies (Brose et al. 2014).

The prevailing fire-oak hypothesis (Abrams 1992, Brose et al. 2001, Nowacki and Abrams 2008) incorporates many causal and contributory influences and proposes approaches to mitigate regeneration challenges, reverse compositional shifts, and maintain oak dominance. The fire-oak hypothesis postulates: 1. Fire has been in integral part of upland oak ecosystems in eastern North America for millennia. 2. Oaks are superiorly adapted relative to other hardwoods to survive a periodic fire regime and exploit the postfire environment. 3. The cessation of a periodic fire regime in the early 1900s is a major cause for the current oak regeneration problem. 4. Prescribed fire can be used in some situations to help regenerate and restore upland oak ecosystems.

Disturbance-succession models describe the influence of the disturbance regime on a forest type dominant tree species (Brose and Waldrop 2010). In addition to fire, many other aspects of the disturbance history of Eastern forests have contributed in different ways and amounts to species composition and dominance. Deforestation for agriculture and grazing, afforestation following farm abandonment, reforestation following clearcuts or fire, various timbering practices and consequences, and introduction of non-native insects and pathogens have altered successional pathways and developmental patterns (Brose et al. 2001). To determine the ecological requirements needed to restore and manage oak forests, it is necessary to consider the influences under which oak forests developed. Complex interactions between climatological conditions, human populations, land-use patterns, and industrial activities define the challenge in comparing the disparate conditions throughout history.

Historic Fire Use

The first tenet of the fire-oak hypothesis is that fire has been in integral part of upland oak ecosystems in eastern North America for millennia (Brose et al. 2001, Guyette et al. 2002, Pyne 1982). Native American hunter-gatherer and agrarian societies used fire extensively to drive and spot game, maintain early successional habitat necessary for the grazing and browsing of game species, and to clear land and recycle nutrients for agriculture (Delcourt and Delcourt 1998). Additionally, the increased post-fire light environments encouraged wild grains, berries, and legumes (Waldrop and Goodrick 2012) and facilitated easier acorn and chestnut gathering by reducing the obscuring groundcover. Fire was also used to maintain travel corridors, as a method of communication, and in wartime tactics. In the central hardwood forests, Native American fire use can primarily be characterized by dormant season, low intensity, frequent return intervals interspersed with fire-free periods. Fire free periods of 10 to 40 years every 100 to 200 years in a periodic fire regime favored oak regeneration and helped create the conditions for successful recruitment and overstory dominance (Brose et al. 2014, Brose et al. 2013, Guyette et al. 2002).

Lightning ignitions have played a limited role in eastern ecosystems. Lightning is frequently accompanied by rain, and supporting evidence includes predominately dormant season burns, when lightening is less frequent. Lightning ignitions during growing seasons occur mostly in xeric (pine-oak-heath, oak woodlands, and grass) dominated ecosystems and areas with frequent droughts (Guyette et al. 2012, Ruffner and Abrams 1998).

The early European settlers saw the benefits of and adopted many Native American land management and burning practices. Fire was used for hunting, land clearing, grazing, and agricultural or swidden farming purposes (Pyne 1982). Broadcast fires were common during this time when burning the land to facilitate grazing or create open areas was a widespread practice. Early settlers and future generations had learned from Native American predecessors that growing season fires effectively maintained herbaceous vegetation beneath an open forest canopy. Not all areas would burn annually, however, giving oak an opportunity to dominate the advance regeneration pool, as other pyrophobic species succumbed. When woodsburning waned, or the land was abandoned or converted to a different use, the cycle of recurrent fire regime followed by withholding fire were the conditions which inherently favored and maintained oak on disturbed sites across the landscape.

During colonial expansion, the severity of the terrain in the Appalachian Mountains limited suitable settlement sites, transportation, land use options, and harvesting feasibility, and created a patchwork of landscape conditions (Hicks 1998). As afforestation followed the trend of farm abandonment, subsequent cutting practices took desirable species in stages at first, but forest product demands and harvest volumes increased with the onset of the industrial revolution. As transportation networks matured and access improved with railroads, larger scale exploitation became standard. During the heavy logging era and the years following, railroads, logging, landowner, and other anthropogenic activities ignited uncontrolled wildfires that burned millions of acres across the eastern forests (Brooks 1911).

Pyne (1982) characterized these historical periods by the relationship between fire and plow, fire and hoof, and fire and axe. Some combinations of these seemingly deleterious local factors and cycles of woodsburning, land clearing for agriculture, grazing, cutting for fuelwood and charcoal production, and logging counterintuitively contributed to a progression of increasing oak dominance. Yet, many forests following this time were described as understocked, unhealthy, and in a run-down condition, owing mainly to fire, disease and insects, and indiscriminate cutting and grazing (Schnur 1937), which would usher in a new approach to forest management practices.

Fire Suppression Policy

Reflecting the anthropogenic trajectories, many factors were transitory yet still strongly shaped the structure and composition of oak forests. Defying the ephemerality of all other historical influences, fire endured. Despite thousands of years of interdependence between fire and maintaining oak forests, fire was thought to be the greatest obstacle to the newly established forestry profession, largely in response to the post-logging conflagrations that burned throughout the United States in the 19th and early 20th centuries (Pyne 2000). In combination with the developing conservation movement, fire prevention and suppression were established as a nationwide mission. Various state-level fire policies had been in existence long before national policies, but the regard for these policies was not always high, was often ineffective or ignored, and inconsistently enforced (Pyne 1982).

Addressing concern that forests were becoming an endangered natural resource, national scale fire suppression policies gained momentum after the Transfer Act in 1905, the Weeks Act in 1911, and the Clark-McNeary Act in 1924. Collectively, these acts transferred land to the USDA to be managed by the Forest Service, established the National Forest system and the purchasing power to increase it, and established co-operative arrangements with state forestry agencies to strengthen fire prevention and suppression programs (Pyne 1984). In addition to Forest Service employees, Civilian Conservation Corps members, state forestry departments, private timber companies, military servicemen, and community members all contributed to fire prevention and suppression efforts (Pyne 1982). Preceded by the 10 am policy in 1935, the introduction of Smoky Bear coincided with a wartime propaganda campaign in 1944 and contributed to the misperception that the existence of fire and forests are mutually exclusive. Forest growth rebounded with fire suppression, abating fears of a timber famine, but there were dramatic changes in the ecological succession, conditions, and functions influenced by fire.

Abiotic Influences

In addition to fire exclusion, other effects have impacted the development of oak forests and contribute to oak regeneration difficulties. White-tailed deer function as a “keystone species” because of the magnitude of their ecological impact on forest community structure and the distribution and abundance of other species (McShea and Healy 2002). Many of the modern oak dominated forests developed in the absence of significant deer populations, but due to reintroduction, hunting policies, and elimination of deer predators, deer populations can now be in excess of the carrying capacity of many forest habitats. Deer impacts are not uniform across the landscape and patterns frequently follow gradients of fertile soils supporting preferred forage, and early successional habitats such as regenerating forests (Rawinski 2014). Oaks and maples are listed among preferred tree species, while sweet birch is listed as low-preference or avoided species and in areas with overabundance, effects of foliage browse and acorn forage can be extremely severe by inhibiting oak regeneration and encouraging regeneration non-browsed species (Rawinski 2014).

The loss of American chestnut is another factor contributing to the evolution of disturbance patterns. Chestnut blight (*Cryphonectira parasitica*) spread to WV in 1909 (Brooks

1911), extirpating chestnut from the overstory in about 40 years. American chestnut was a dominant species across the Allegheny Mountains and the effects of its loss on oak forest dynamics were extensive. Chestnuts were a reliable seed producer every year and provided a stable and abundant source of mast for wildlife that complemented the periodic contributions of beech, oak, and hickory (*Carya* spp.) species. Provided by the prolific ability to sprout and quickly respond to newly available resources (Belair et al. 2014), chestnuts and the associated forest cover were highly dependent on disturbance events, including fire. Fire has been implicated in the increased abundance of chestnut in the Appalachians before the blight (Delcourt and Delcourt 1998). Chestnut is thought to be intermediate to shade-tolerant, and red maple, which was historically not a major component of this forest ecosystem, has captured available understory growing space (Wang et al. 2013). Thus, the composition of many forests once containing a major component of chestnut are succeeding from an oak-hickory dominated association to one dominated by maple or shade intolerant species (Abrams 1998, Nowacki and Abrams 2008). It is also thought that chestnut may have some allelopathic qualities. Several studies have shown that leachate from leaf litter may limit the germination and development of roots, stems, and leaves of some common competitors including red maple, sweet birch, yellow-poplar, and Eastern hemlock (*Tsuga canadensis*) (Vandermast et al. 2002, Wang et al. 2013). The extent of these effects in suppressing competition in a forest setting is unknown, but perhaps the forest floor environment is no longer as oppressive to those competitors.

The influence of one or more of the aforementioned factors have caused ecological impacts have been widespread in nearly all of the forest types that include oak. The successional pathways created by historical land use in combination with differences attributable to physiographic regions, and their associated influences on species composition, shaped a mosaic of forest conditions. Hence, there is not a uniform approach to maintaining oak on different sites, but instead there are silvicultural guidelines based on stand-specific conditions and oak ecology.

OAK ECOLOGY AND SILVICULTURE: FUNCTIONS AND ROLE OF FIRE

Oak Ecology and Physiological Adaptations to Fire: Germination, Root Development, Early Growth, Sprouting Ability, Fuel Array, Bark Characteristics and Decay Resistance

Addressed in the second tenet of the fire-oak hypothesis is that oaks are superiorly adapted relative to other hardwoods to survive a periodic fire regime and exploit the post-fire environment (Van Lear and Watt 1993, Brose et al. 2001, Nowacki and Abrams 2008).

Most of the hardwood oak associates are able to sprout, but it is the ability to sprout following repeated burns that has earned oak the “fire persistent” description (Johnson et al. 2009). Oaks have several traits that are beneficial at different times in their life cycle to be persistent in frequent return interval fire regimes including acorn receptiveness to fire-prepared seedbeds, hypogeal germination, taproot growth, sprouting ability, thick bark, and decay resistance (Abrams 2006). However, these traits do not bestow an advantage in a fire-excluded environment, and the inability to tolerate dense shade and slower early growth rate than competing species have proven to be causing a severe management challenge on better quality sites. Oaks possess several physiological adaptations that provide a disposition to intrinsically accumulate and occupy lesser quality sites not able to sustain other species, easing regeneration challenges (Johnson et al. 2009).

Oaks undergo hypogeal germination, wherein cotyledons remain inside the seed coat and provide an energy source during seedling development (Kramer and Kozlowski 1960). Mineral soil is a poor conductor of heat (Iverson and Hutchinson 2002) and hypogeal germination results in a lower root collar location in the soil, providing dormant buds more protection during a fire (Brose and Van Lear 2004).

Acorns of both oak groups require sufficient moisture content to prevent desiccation but the red oak group can tolerate lower levels to maintain germinative capacity relative to other species (Korstian 1927). Although a leaf litter cover is important to help maintain seed moisture content, if it is too thick it can inhibit germination. Deep litter can prevent both the radicle from reaching mineral soil as well as epicotyl emergence (Dey and Fan 2009). The litter layer can be reduced following a surface fire and seedbeds usually have areas of exposed mineral soil, potentially creating favorable conditions for acorn germination and seedling establishment (Johnson 1974, Brose et al. 1999a). Furthermore, the post-fire seedbed can be less favorable for other non-oak species to germinate if it has been xerified and does not have sufficient moisture. Areas of thin litter are preferred by squirrels (*Sciurus* spp.), birds, and other vertebrates for acorn burial (McShea and Healey 2002).

The relationship between oak forests and wildlife is reciprocal and includes elements of predation and promotion. Acorn consumption impact is partially offset by the benefit of dispersal and burial. Frequently, acorns are either damaged by insects, fungi, or bacteria, partially or wholly consumed by wildlife, or otherwise unviable (Gribko et al. 2002). Grey and fox squirrels (*Sciurus niger* and *S. carolinensis*) that cache acorns of the white oak group frequently excise the embryo before burial, preventing carbohydrate diversion from the cotyledons to the taproot (Edwards et al. 2003). However, unrecovered and undamaged acorns buried in the soil can potentially bestow a benefit of reduced exposure to lethal temperatures pre- and post-germination. Cached acorns are frequently buried < 2 cm below the soil surface or covered with leaf litter (Edwards et al. 2003), which facilitates a more protected location from which the acorn has a better chance of remaining viable, or a more protected root collar location from which the dormant buds can sprout post-fire (Brose and Van Lear 2004, Greenberg et al. 2012).

In addition to germination, a change in soil microclimate can influence soil biota and fine root function. Studies indicate that fire xerifies the soil through increased solar radiation from sapling density reduction, increased heat absorption at the soil surface from blackened litter or exposure, increased evaporation, and decreased soil moisture and water infiltration (Van Lear 1991, Barnes and Van Lear 1998). It has been found that these effects are not as pronounced and have a shorter duration on mesic sites, especially after full emergence of ground and canopy cover, with elevated temperature effects lasting about 75 days on mesic sites and nearly 155 days on xeric sites (Iverson and Hutchinson 2002).

Physiological adaptations that provide a disposition to occupy droughty and less fertile sites include a taproot that provides greater access to nutrient and water resources (Crow 1998, Lyford 1980). The large root:shoot ratio developed by a conservative growth strategy is beneficial during droughts, on less fertile sites, and when repeated sprouting is necessary, but may disadvantage oak when it competes with species having more exploitative strategies favoring shoot growth (Johnson et al. 2009).

Even a single low intensity fire is sufficient to kill seedlings stems but most hardwood species have the capacity to sprout from surviving root systems. The capacity to sprout varies by species but tends to increase with size (Dey and Hartman 2005). Both aforementioned silvical characteristics of hypogeal germination and taproot development contribute to oaks consistent ability to sprout (Barnes and Van Lear 1998, Brose and Van Lear 1998). For similarly sized trees, oak and hickory are more likely to survive than some of their competitors such as sugar (*A. saccharum*) and red maple, sweet birch, and yellow-poplar (Brose and Van Lear 1998, Dey and Hartman 2005)

The ability to persist in a low interval fire regime is attributable to not only the preferential allocation of biomass to the root system that benefits sprouting, but to the soil insulation properties that enables survival of the root system. Iverson and Hutchinson (2002) examined soil temperatures in prescribed fires in Ohio on both xeric and mesic sites. Average probe temperatures from the fire were 222 °C (431 °F), which caused soil temperatures to increase by an average of 9.6 °C (49 °F) for an average duration of 5.6 minutes. Additionally, heat penetration typically stays close to the soil surface. For example, 59 °C (138.2 °F) at a depth of < 2.0 cm was reported in the southern Appalachians (Elliott and Vose 2006). Soil temperatures of 40 to 70 °C (104 to 158 °F) are required to cause significant biological effects, and surface fires are estimated to transfer to the soil only about 5% of the heat they release (Iverson and Hutchison 2002).

Site-specific species composition dictates leaf litter and coarse woody debris type and arrangement, and corresponding decay rates can vary widely. Fuel load quantity and composition are major drivers of fire behavior and intensity, and the fuel array in oak dominated stands can help promote fire frequency and intensity levels necessary to be effective (Barnes and Van Lear 1998, Johnson et al. 2009). In oak forests where fallen leaves curl and resist decay, a highly aerated and flammable fuelbed develops, encouraging more frequent and intense fire. Leaves of fire-sensitive species such as American beech, yellow-poplar, and maple lie flat and decay rapidly, preventing development of a fuelbed suitable for combustion and spread, thereby discouraging or inhibiting fire (Van Lear et al. 2000). Compared to oak species, Stottlemyer et al. (2010) found red maple and beech leaves have a lower calorific value, a measure of the thermal energy released when a fuel is burned, and higher mineral ash content, which affects combustible fuel mass, gas evolution, and ignitability; properties that result in lower fire intensity and decreased flammability. The same species patterns also tend to occur on xeric and mesic sites, the features of which also promote or discourage fire from the influence of topography and its effects on soil moisture and shading. In the absence of fire, plant communities adapted to fire are likely to be eventually replaced by plant communities not adapted to fire (Van Lear and Watt 1993). In addition to species conversion, another aspect of the feedback loop of “mesophication” (Nowacki and Abrams 2008) is that decomposition is faster on mesic sites, reducing total and available fuel levels. The faster decay rate of mesophytic leaves comparatively reduces fuel level inputs per square foot of basal area (Hicks 1998). Thus, total fuel levels are reduced because of faster decomposition, and available fuels for combustion are reduced because of decreased flammability and the high moisture of extinction. Moisture of extinction is the moisture content of the fuel at which a fire will not spread (Rothermel 1972).

Bark thickness and furrowed characteristics provide cambial protection and insulation, which make larger size oaks resistant to low to moderate intensity fires (Schafer et al. 2015, Kramer and Kozlowski 1960). Stem diameter has been shown to be significantly correlated to tree survival after fire, indicating that as bark thickness increases, a tree's fire resistance increases (Dey and Hartman 2005, Yaussy and Waldrop 2010, Yaussy et al. 2004). Oaks have the ability to compartmentalize wounds and limit the spread of decay (Smith and Sutherland 1999) if fire intensity is sufficient to cause damage to the bole. Tyloses in white oaks contribute to greater compartmentalization ability than that of red oaks (Johnson et al. 2009). At larger sizes yellow-poplar has effective bark insulation properties (Wiedenbeck and Schuler 2014), but at small sizes it is very sensitive. Sweet birch is easily damaged by fire at all sizes because it has thin bark (Lamson 1990).

While fire will inevitably lead to some oak mortality, characteristics at different development times contribute to oak's persistence in a periodic fire regime.

Oak Silviculture

The paradox of a species that is dominant on the landscape, yet difficult to regenerate at the stand level (Crow 1998), has compelled examination of oak community competitive dynamics and the mechanisms influencing the establishment of oak seedlings (Gribko et al. 2002).

Coinciding with the exclusion of fire, oak regeneration and recruitment challenges have been experienced in managed and unmanaged stands on mesic sites (Carvell and Tryon 1961, Schuler and Miller 1995, Weitzman and Trimble 1957). In oak dominated systems on more xeric sites, oak advance reproduction accumulates over time that can compete successfully after disturbance, whereas in recalcitrant mesic ecosystems, oak reproduction may accumulate only after recurrent disturbances coinciding with successive acorn crops (Johnson et al. 2009). Oak forests are frequently referred to as disturbance-mediated and were sustained by a unique combination disturbances of varying scale and frequency, high understory light levels, and low levels of understory competition (Rentch and Hicks 2003). In the absence of disturbance, dense shade develops and oak seedlings seldom survive from one cohort to the next; eventually being successionally displaced by different species (Carvell and Tryon 1961).

Despite general consensus that fire played a role in establishing the oak-dominated stands in the late 1800s and early 1900s (Brose et al. 2001, Guyette et al. 2002, Hutchison et al. 2008, Schuler and McClain 2003), there was still a need for standard silvicultural guidelines that use fire to regenerate oak (Barnes and Van Lear 1998, Van Lear 1991). Since about 1950, conflicting conclusions have steadily amassed debating whether fire is beneficial or detrimental to oak regeneration; however outcomes were frequently reported from widely different stand conditions, physiographic regions, and with different fire characteristics (Brose et al. 2014).

The final component of the fire-oak hypothesis is that prescribed fire is effective to help regenerate and restore oak ecosystems in certain situations (Brose et al. 2014, Stout et al. 2012). Broadly, fire can serve in silvicultural application to alter light levels, seedbed conditions, and species composition. The technical aspects regarding if, how, and when fire fits into the regeneration process have developed with extensive effort and collaboration in the last 40 years, and studies with conflicting results have been analyzed and synthesized by commonality to further refine guidelines (Brose et al. 2006, Brose et al. 2014, Dey and Hartman 2005, Dickinson 2006, Waldrop 2014, Waldrop and Goodrick 2012, Yaussy 2000).

Synthesis has revealed that overall, fire reduces the number of small diameter stems in the midstory, promotes establishment of new oak seedlings, preferentially selects oak reproduction over its mesophytic competitors, and reduces height differences between these species (Brose and Waldrop 2014). Generally, prescribed burning is most effective to favor oak when conducted during the growing season, when intensities are moderate to high, and as part of a treatment sequence that includes a substantial reduction in overstory density and may include multiple burns (Brose et al. 2013). However, dormant season burns may be the only option if surface fuel moisture levels during the growing season at a site precludes the ability to burn. An outcome of early experiments was the “shelterwood-burn technique” (Brose et al. 1999b), combining two disturbances designed to create conditions favoring oak regeneration. Post-harvest burning has been proposed as a potential alternative to the shelterwood-burn to avoid the risk of damage or mortality to overstory trees (Brose 2013, Ward and Brose 2004). The oak-fire hypothesis has been the subject of stimulating discussion since propounded (Arthur et al. 2012, Dey and Fan 2009).

In response to regeneration and recruitment challenges, silvicultural recommendations for site preparation, intermediate treatment, and harvest methods have been tailored specifically to promote oak over other species (Loftis and McGee 1993). Competition among various species determines future stand composition (Brose et al. 2008), and reflects characteristics of the site including moisture, topographic position, soil, disturbance or management history, and species' silvical characteristics (Trimble and Weitzman 1956). Red maple, sweet birch, yellow-poplar, and red oak are ecological antagonists; depending on the disturbance regime, conditions are created that favor them selectively. The silvical characteristics of these common oak competitors help explain how they have been successful at displacing oak on mesic sites.

Red maple is one of the most abundant and widespread trees in eastern forests and is purported to thrive on a wider range of sites, soil conditions, and elevations than any other tree species in North America (Walters and Yawney 1990). Flexible germination requirements, biennial good to bumper seed crops, and the ability to germinate and persist with very little light are particularly beneficial. The strategy of seedling accumulation under a closed canopy has allowed red maple to flourish on both xeric and mesic sites (Abrams 1998, Hicks 1998, Lorimer 1984).

Similar to oak, sweet birch is intermediate in shade tolerance and can respond positively to increased light levels following fire or partial reductions in overstory density (Schuler and Miller 1995, Thomas-Van Gundy and Schuler 2008, Trimble 1975). Also, the reduced litter layer of post-fire seedbeds can be very conducive to sweet birch seed germination if the fire and the topographic position do not create xerified conditions.

Yellow-poplar is a prolific seed producer and can achieve and maintain a dominant position in the overstory by its rapid and sustained height growth early in stand development (Beck 1990). On high quality sites, yellow-poplar has exhibited the greatest increase in species importance among its common associates following stand initiating disturbance events through early stem exclusion (Brashears et al. 2004). Yellow-poplar can be a long-lived species, which makes it a formidable competitor in all stages of succession in even-aged management schemes.

Depending on numerous factors, the regeneration process can last from 10 to 30 years in even-aged management and because this process starts in the mature forest stage, long-term goals for species composition need to be identified before the stand initiation stage (Dey et al. 2007). This process broadly consists of 3 major phases; acorn production, establishment of acorn origin seedlings, and seedling development into competitive reproduction, followed by a timely release of the competitive reproduction (Hicks 1998, Johnson et al. 2009). The requirements of having competitive sources of oak regeneration, followed by a timely, sufficient release, are so fundamental that they have been termed the “laws” of oak silviculture (Loftis 2004). In addition to manipulations during establishment, management objectives for the oak component of future stands also determine the need for tending and release treatments for oak in the intermediate stages of stand development (Rentch et al. 2009).

Following a canopy disturbance, the three sources of regeneration include new seedlings from seed stored in the forest floor, stump, shoot, or root sprouts, and advanced seedlings present in the understory (Dey et al. 2007). To enhance the regeneration potential for oaks, silvicultural intervention at the most basic level must alter the stand structure and light environment, allowing oak to grow into larger advanced reproduction and making it able to compete after release, and reduce the competition from other species. Reducing competition from other species can involve altering the stand structure and light environment in such a way that accommodates inherent differential species response, or directly reducing competing regeneration with other methods including mechanical treatments, or herbicide (Loftis 2004, Schuler and Stephens 2010).

Oaks are intermediate in shade tolerance, with northern red, black, and scarlet being less shade tolerant than white and chestnut oak (Sander 1990), and insufficient light is a primary cause of oak regeneration failure. Light levels are so low in the understory of fully-stocked, mature forests that respiratory demands for development of large advanced reproduction are not met (Lorimer 1993). The shelterwood method is advocated to control understory competition and light levels through manipulating mid- and overstory density through sequential cutting (Johnson et al. 2009). Cutting sequences can involve 2 or 3 steps including a preparatory cut, which may not be necessary in all stands, the first removal cut, and the final removal cut. A preparatory cut may be necessary to remove undesirable species, unacceptable growing stock, and seed sources aggressive competitors. The first removal cut, or seed cut, provides a suitable light regime for oak regeneration to grow to a competitive size over the next few years without giving too much encouragement to shade intolerant species. After a shelterwood cutting, below canopy irradiance can increase to more than 20% of full sunlight, which increases seedling growth and leaf area (Gottschalk 1985, Gottschalk 1994). At a relative density largely determined by site quality, it is necessary to retain merchantable size oak stems as a seed source and for shade they will provide. The final removal cut removes the residual overstory trees to provide the high light environment for the competitive oak regeneration already in place (Brose et al. 2008).

The interactions of microclimate and edaphic factors, the morphological and physiological characteristics of the species present, and the factors limiting successful regeneration guide silvicultural prescription development (Hodges and Gardiner 1993). For example, caution should be exercised on high-quality sites that contain a significant component of sweet birch and yellow-poplar, as yellow-poplar can regenerate in abundance from dormant seeds and has proved to be a formidable competitor (Steiner et al. 2008). Preparation for a successful regeneration begins many years before a harvest, and assessing the regeneration potential of understory and overstory contributions is necessary to predict if oak will represent an adequate component in the new stand, be able to compete during stem exclusion, and maintain its codominant or dominant position in understory reinitiation (Loftis 1990a, Sander et al. 1976). Beyond assessing the regeneration potential, a pre-harvest inventory identifies interfering vegetation and deer browse, which may necessitate competition control and fencing. Using data collected during inventory, dichotomous decision charts and software programs provide direction in developing a site-specific prescription (Brose et al. 2008) and identifying the necessary manipulations of stand structure in the overstory, midstory, or understory (Carvell and Tryon 1961, Hannah 1987, Loftis 1990b).

The shelterwood system has shown to benefit oak seedling regeneration and recruitment in many stands, however establishment failures were still being experienced elsewhere, confirming that shelterwood residual stocking levels alone could not ensure success (Schuler and Miller 1995). The use of fire to ameliorate seedbed conditions for germination and reduce understory competition had frequently been suggested to employ in an effort to mitigate these problems (Lorimer et al. 1994).

The “Shelterwood-burn” Technique

Critical to success in meeting regeneration objectives, is a comprehensive consideration of factors contributing to, or preventing, the future stand conditions. Initially, the appropriateness of a prescription including fire is evaluated by the effect it will have relative to other treatments or no treatment. Illustrative of the complexity of implementing fire in a management plan is the extensive list of interrelated factors and underlying mechanisms that determine its effectiveness, including sequential order, timing, season, intensity, and frequency. Important site characteristics include the successional stage, structural features and light levels, species and seedbank composition, and xeric or mesic disposition (Brose et al. 2014).

The influence of prescribed fire is identified to be beneficial in two locations of the sequential order of silvicultural treatments in the shelterwood-burn technique. A seedbed preparation burn is proposed for amelioration of the seedbed for acorn germination, and reduction of interfering competition. Interfering competition frequently consists of a dense layer of shade-tolerant understory vegetation that will inhibit oak seedlings following the seed cut of the shelterwood (Schuler, T.M. et al. 2013). Populations of insects that compromise acorn germination, specifically *Curculio* and *Conotrachelus* weevils, may be affected by fire but to what extent on a large-scale is lesser known (Oak 1993, McCann et al. 2006). Depending on site circumstances, a site preparation burn may or may not be necessary.

Following a reduction in the overstory, a release burn conducted in mid to late spring can free competitive oak from more vigorous species or other interfering vegetation. The release burn can be conducted either before or after the final removal cut. When conducting a seedbed preparation burn or a release burn, the amount of time necessary to wait following establishment of a new cohort or overstory reduction depends on overstory density, species composition, and site quality (Brose 2008).

Acorn production and germination are the first steps in the regeneration process. Acorn periodicity can contribute to timing complexities when management plans include fire, as burn windows are already short in mesic eastern forests. Given the negative effects of conducting a burn after a bumper acorn crop and the lack of carry-over or a robust seed bank (Sander 1990), careful burn plan choreography is necessary. Acorns of the red oak group species germinate in the spring after a period of dormancy and cold stratification, while the white oak group starts in the fall. Although fire can improve the seedbed conditions, fall burns can lower germination rates by "cooking" the acorns and rendering them unviable (Auchmoody and Smith 1993, Korstian 1927). Low intensity burns reduce the viability of acorns on the leaf litter surface, but the effect is reduced on acorns protected by duff or mineral soil (Greenberg et al. 2012). It is suggested to attempt timing a burn just before a good acorn crop year or delay burning for several years until seedlings from a bumper crop are established. This new cohort will then provide managers an opportunity to manipulate the conditions for oaks to secure a competitive position (Loftis 1990b).

Season of burn is functional in determining the expected seedling response to fire, although burn window availability may preclude the option to choose between a growing or dormant season burn. Sprouting is frequently more vigorous for all species following dormant season burns because of reduced physiological activity and greater carbohydrate reserves (Dey and Hartman 2005). Additionally, dormant season burns are less likely to heat the soil to lethal temperatures because typically ambient air and soil temperatures are lower and moisture levels are higher. The alignment of this combination of factors may likely decrease the effect on reducing oak competitors. Barnes and Van Lear (1998) found that there was no significant difference in oak density from three dormant season burns versus one growing season burn, although the growing season burn was more effective in reducing yellow-poplar. Even with periodic and annual winter burning oak stems tend to increase at the expense of other hardwoods (Van Lear and Watt 1993). Leaf expansion by oaks is typically later than other species, so if feasible, an ideal time to burn could be the window between competing species and oak leaf-out.

Fire frequency is determined in an assessment by season of burn, regeneration species composition and structure, and objectives. As with a dormant season burning, single burns on productive sites are unlikely to enhance the competitive position of oak regeneration, necessitating multiple burns (Johnson 1974, Teuke and Van Lear 1982, Wendel and Smith 1986). In young stands, fire-free period is necessary for succession to proceed beyond stand initiation.

Fire intensity differentially affects ecosystem responses, including soil erosion, faunal perturbation, vegetation regeneration, and community structure restoration (Keeley 2009).

Typically death of plant cells occurs at temperatures > 50 to 55 °C (122 to 131 °F) for a short time, or lower temperatures for a longer duration, thus, cool fires with slow rates of spread can be as lethal as faster-moving hot fires (Waldrop and Goodrick 2012). Regeneration and restoration efforts hinge on the physiological response to the fire environment, which if too severe, can undermine the intent. Xeric and mesic site characteristics are influential on fire intensity attributable to fuel composition and moisture levels, topography, and air temperature and humidity (Elliott et al. 1999). Areas with significant logging debris could burn or smolder long enough to increase soil temperatures to detrimental levels, potentially necessitating site preparation to control fire intensity and overstory damage.

The economic impact of timber damage is one of the main concerns having prevented prescribed fire from being integrated into silvicultural systems on an operational scale in the central hardwood region. Damages are frequently visible on the uphill face of the tree after a fire and potential negative effects on quality and vigor present legitimate cause for hesitation in employing its use (Wendell and Smith 1986). However, Marschall et al. (2014) have found that with site preparation to minimize damage, fire damage contained to the bottom 50 cm of the butt log and on less than 20% of basal circumference of trees that are a minimum of 20 cm dbh, fire damage can result in low timber value loss if harvested within 14 years. They also found value loss is very low if trees are harvested within about five years after fire damage, regardless of scar size. Wiedenbeck and Schuler (2014) found that of red and white oak, red maple, and yellow-poplar, red maple was the most prone and yellow-poplar the least prone to fire damage and grade or scale reducing defects. The relationship between species and the occurrence of tree grade- or scale-reducing defects is thought to be influenced by bark thickness differences and the insulation it provides from temperature extremes (Wiedenbeck and Schuler 2014). These studies illuminate the importance of understanding the economic impact of burning a stand with some of the most valuable logs still on the stump and may not be harvested for decades. Another consideration is the marketability of a stand that has been burned and the negative perceptions about quality, justified or not, that the buyer would understandably have. A potentially viable alternative to the shelterwood-burn, when there is concern of damage or mortality to overstory trees, is a post-harvest burn (Brose 2013, Ward and Brose 2004).

Pursuant to the prescription, the subsequent burn plan delineates operational procedures and the firing pattern can be altered according to desired fire intensity. A balance must be reached between being intense enough to be effective, yet not so intense that that the fire undermines its ecological purpose. This descriptive and process-based approach will also serve as a reference for other managers to examine relationships between site variables, fire metrics, and vegetation response (Keeley 2009).

Fernow Experimental Forest History and Research Focus

Located in the Allegheny Mountains of north-central West Virginia, the Fernow Experimental Forest is in the northern part of the Monongahela National Forest. The Allegheny Mountains were mapped by Kuchler as spruce-fir, northern hardwoods, mixed mesophytic, and oak-hickory-pine, influenced strongly by elevation and aspect (Kuchler 1964). Red spruce (*Picea rubens*) and northern hardwoods including American beech, yellow birch (*Betula alleghaniensis*), sugar maple, and Eastern hemlock can be found at higher elevations (>900 m). Red spruce restoration efforts are underway as this species is now found on only a small fraction of the original area following harvesting, fire, and growing site degradation (Rentch et al. 2010). The future of Eastern hemlock is threatened by hemlock wooly adelgid (*Adelges tsugae)*, and climate change may have a long-term impact on species composition. Impact models in the region project a potential decrease in species such as American beech, sugar maple, red spruce, and Eastern hemlock (Butler et al. 2014). The Fernow is primarily a hardwood forest perhaps best described as mixed-mesophytic (Braun 1950).

In addition to the aforementioned factors influencing oak forest development and successional pathways, much about current stand conditions can be revealed by examining its management and land-use history. Of German descent, Bernhard Fernow was a pioneer of early forestry in the United States. The eponymous forest has played a significant role in various disciplines of forestry since its purchase by the Forest Service in 1915 and its designation for research in 1934 (Adams et al. 2012).

The mountainous terrain was not suitable for agriculture and consequently was not subject to the deforestation and afforestation land-use cycle common at that time, leaving nearly the entire tract in timber (Adams et al. 2012). Trimble (1977) provides some history while the area was still in private hands in the early 1900s. Railroad construction supported the logging that first took place from 1903 to 1911 and facilitated heavy cutting of accessible and merchantable timber. Providing a glimpse of the original forest he notes, “On lower elevations, the forest was mainly hardwoods with hemlock in mixture along creek bottoms and north slopes. The higher ridges were covered with an excellent stand of spruce and hemlock, while in small patches on the tops of the mountains were pure spruce stands.” Post-logging he reports, “ This land has not been cut as close as many tracts in the region and a few hundred of beech, birch, and maple remain….There have been no fires since logging started and good growth of chestnut, chestnut oak, and black oaks are coming in. On small areas good stands of chestnut poles, 6 to 8 inches were noted….Light logging and no fires have given the forest a good chance to build up and recovery will be rapid if fire is to be kept out."

In contrast to post logging fires elsewhere, this area came under Forest Service protection soon after the original cutting so fires were not widespread, but some stands had been burned-over (Trimble 1970). As part of the fire-prevention efforts, the Civilian Conservation Corps established a 15 ft firebreak around the exterior of the forest and along many ridges in the interior (Trimble 1977). In other areas of the Appalachians the logging associated fires from about 1880 to 1920, notably those in the red spruce zone above 3,500 ft burned so severely that several inches of organic matter was removed, exposing the roots and rocks below (Brooks 1911).

At the time of European settlement, herbivores and carnivores in the Allegheny Mountain region included bison (*Bison bison*), elk (*Cervus elaphus*), black bears, grey wolves (*Canus lupus*), fishers (*Martes pennanti*), and cougars (*Puma concolor*). Except for black bears, all were extirpated during the 1800s from hunting, trapping, and land conversion to agriculture (Adams et al. 2012). The Fernow now supports 48 species of mammals, 92 species of birds, including residents and migrants such as neotropical migratory songbirds, 18 species of amphibians, and 8 species of reptiles (Madarish et al. 2002). The areas that are now mature forest regenerated after cessation of logging and developed without the influence of deer herbivory (Adams and Kochenderfer 2014).

Wind events are the current primary disturbance agents, however ice storms and early snow before leaf abscission have also been influential (Adams and Kochenderfer 2014). Current and potential insect and pathogen threats include gypsy moth (*Lymantria dispar*), hemlock wooly adelgid, emerald ash borer (*Agrilus planipennis*), butternut canker (*Sirococcus clavigignenti-juglandacearum*), dogwood anthracnose (*Discula destructive*), beech bark disease, Duch elm disease (*Ophistoma ulmi*), and chestnut blight (Adams et al. 2012). American chestnut was once an important constituent, however the chestnut blight reduced stand volume by 25% in the 1920s and eventually extirpated the species from the overstory by 1948 (Schuler and Gillespie 2000). These influences undoubtedly shaped in part the current species composition and are illustrative of the many exogenous and abiotic factors that affect the development of the oak forests.

Studies in the Fernow have included many objectives related to timber and watershed management and several early projects involved various silvicultural management schemes. Several notable studies starting in the late 1940s and 1950s included cutting practice levels, site-quality assessments, and their influence in determining early reproduction, species composition, growth rates, and stand development. The integration of several growing-site factors in determining productivity and upland oak site indices were used to help predict the forest response to treatment (Trimble and Weitzman 1956). Observations at that time noted the concerning problem that young oak stems were being out competed by faster growing species early in stand initiation. Also notable was that sweet birch became the most numerous species, which represented about 17% of basal area of stems 12.7 to 27.9 cm (5 to 11 in) after 20 years of uneven-age management; it was predicted that stands subjected to partial harvesting would eventually be dominated by shade tolerant species (Trimble 1965, Trimble 1970).

The Fernow is now managed by the Northern Research Station. The research work unit is referred to as NRS-01 (Ecological and Economic Sustainability of the Appalachian Forest in an Era of Globalization). The mission is to *develop timely, relevant knowledge and provide management guidelines to sustain and enhance the ecological and economic function and value of Appalachian forests in the context of changing environments and human values* (Adams et al 2012).

The study described herein is part of a more comprehensive examination of the efficacy of prescribed fire to regenerate oak on 2 mesic mixed-oak sites using the shelterwood-burn technique (Brose et al. 1999b), the early results of which were encouraging in the Virginia Piedmont. Two seedbed-preparation burns were conducted in 2002/2003 and 2005 to eliminate the dense shade tolerant understory layer that would inhibit a positive oak regeneration response following the first stage of the planned shelterwood harvest. In 2009-2010, the seed cut of the shelterwood sequence reduced overstory basal area from 145 to 62 ft^2/ac, and from 108 to 44 stems/ac (dbh >5.0 in). Also part of the experimental design are deer exclosure fences to examine the effects of herbivory, and control plots to serve as an unburned comparison. More detail on the previous stages and other aspects of this study can be found in Schuler et al. (2010), Schuler, T.M. et al. (2013), McCann et al. (2006), Rowan et al. (2005), and Ford et al. (2010).

The methods and results herein address the first growing season survival and growth from the 2014 release burn treatment that was applied in response to oak regeneration predictably being outcompeted by other species (Figure 1).

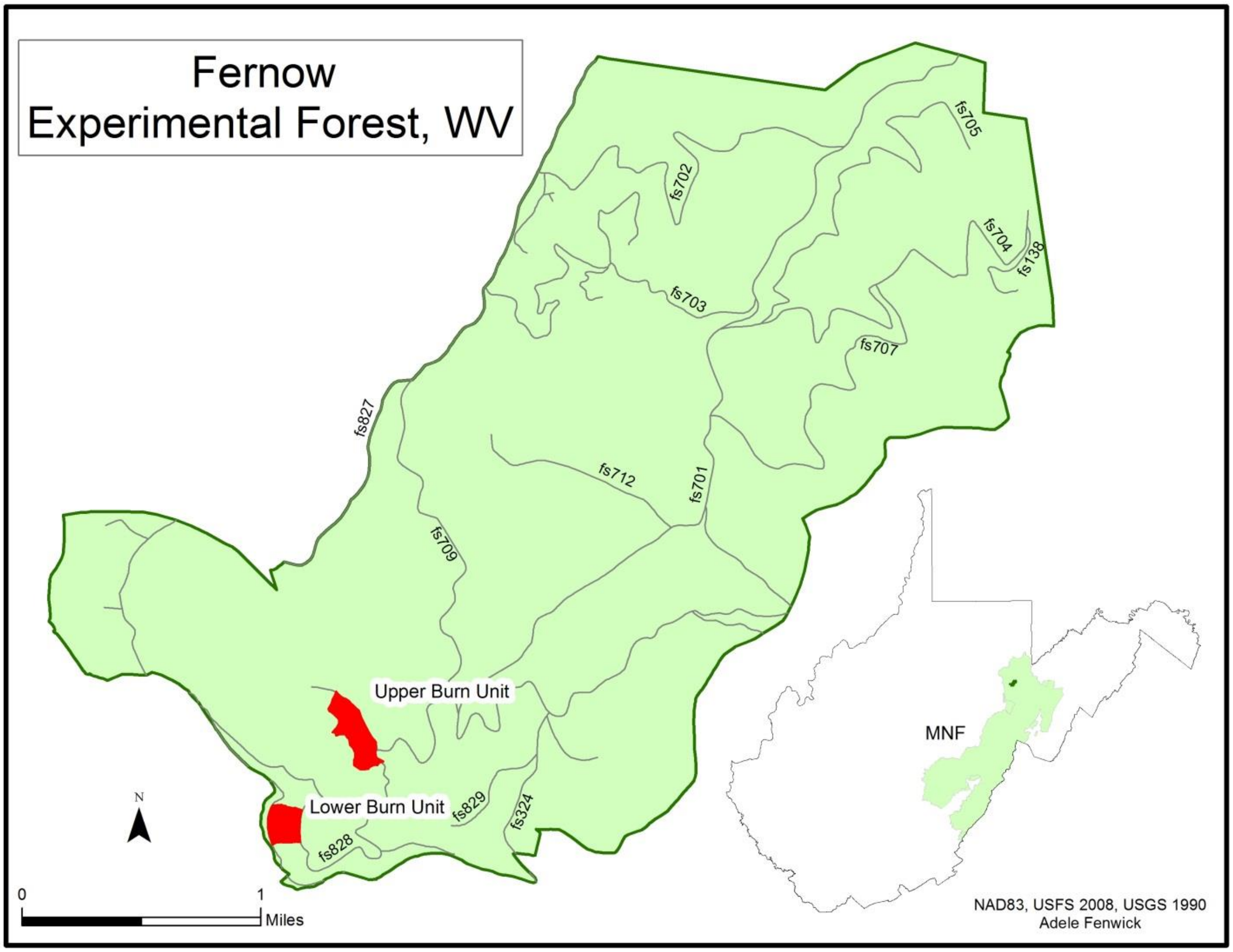

Figure 1. Study site locations of 3 prescribed fires in 2002/2003, 2005, and 2014 on the Fernow Experimental Forest within the Monongahela National Forest (MNF).

The purpose of this component of the larger project is to contribute to the technical merits and guidelines for using prescribed fire to benefit oak seedling establishment and release from red maple, sweet birch, and yellow-poplar competition. Of particular interest is how fire affects species survival and growth rates, and ideally provides oak the ability to maintain a superior position through the competitive sorting process during stand initiation (Johnson et al. 2009).

Species-specific seedling survival probability and growth models as a function of size were developed to enable determination of probable seedling response to, and subsequent sprout growth after, a fire treatment. These models are intended to provide support for the use of fire in management activities and more reliably predict its effects. Also examined was the degree to which pre-burn size could predict first year post-burn growth.

METHODS

Study Area Description

The Fernow is in the Allegheny Mountains section of the Central Appalachian Broadleaf Forest and is characterized by high, sharp ridges, low mountains, and narrow valleys (McNab and Avers 1994). Burn site elevation of the study area is from 613 to 774 m (2,010 to 2,540 ft). Annual precipitation on the Fernow is distributed evenly throughout the year and averages 148 cm (58 in), of which about 14% is snow. Mean annual temperature is approximately 9 °C (48 °F). The growing season is about 149 frost-free days from May to October, with leaves beginning to emerge in in late April and beginning to fall in late August or early September (Adams et al. 2012).

The most common soil on the Fernow is Calvin channery silt loam, which is derived from acidic sandstone and shale, is well drained, moderately permeable, strongly acid to very strongly acid, and natural fertility is moderate to moderately low (Adams et al. 2012). Soils in the study area are Calvin channery silt loam with a minor inclusion of Gilpin channery silt loam, which is moderately permeable, very strongly acid to extremely acid, and has moderately low fertility (Schuler, T.M. et al. 2013). Mean annual soil temperature regimes are mesic, although frigid soils have been found at the higher elevations (Crews and Wright 2000). Streams dominate the surface water hydrology on the Fernow and most are ephemeral or intermittent until becoming perennial channels farther downstream (Adams et al. 2012). The Fernow is situated between Shavers Fork and Black Fork in the Cheat River Watershed (Kochenderfer et al. 2007).

Characteristic species on the Fernow include upland oaks, with northern red oak being most abundant, but also include chestnut, white, scarlet (*Q. coccinea*), and black oak, yellow-poplar, black cherry, maples, sweet birch, American beech, hickories, basswood (*Tilia americana*), blackgum, sassafras (*Sassafras albidum*), and white ash (*Fraxinus americanca*). The natural conifer component consists of Eastern hemlock and scattered red spruce (Madarish et al. 2002). The study area could more specifically be described as mesic mixed-oak. Oak overstory species, represented in decreasing order of basal area, include northern red, chestnut, and white oak, and common associates include red maple, sugar maple, sweet birch, and yellow-poplar (Schuler, T.M. et al. 2013). Based on site index_{50}, most areas on the Fernow are fair to excellent site quality, with oak site-indices from 60 to 80. The study area site index is 70 for northern red oak and is characterized as a good site (Schnur 1937).

Experimental Design

Using a subset of the existing overstory plots, seedling response plots were established in 10 overstory plots measuring 0.2 ha (0.5 ac) that were treated with prescribed fire. Five of the overstory plots were fenced and 5 were unfenced, facilitating the examination of deer herbivory effects. Within the previously established overstory plots, seedling response plots were systematically distributed at the corners and middle, and collocated at 0.0004 ha (0.001 ac) plots marked with rebar. Five seedling response plots per overstory plot resulted in 50 total seedling response plots. Plot radius was extended outward to a distance necessary to measure sufficient sample seedlings, resulting in variable plot sizes from about 3.5 to 4.6 m (10 to 15 ft).

Data Collection

Pre-burn seedling response plot measurements included species, stem height, ground line diameter, and presence of competition. The stem was considered free-to-grow if it did not have any presence, arboreal or non-arboreal, in a vertical conical area at a 45 degree angular extension from the terminal bud of the measured seedling stem. The species of the largest individual in said cone was determined to be the “worst aggressor”.

The measurement sizes in the existing experiment define seedlings as <25.4 mm (1 in) dbh, and saplings as 25.4 mm to <127.0 mm (5.0 in) dbh. To more rigorously examine the response of small reproduction, the goal of this study was to measure 12 to 16 stems within each of the newly established seedling response plots, consisting of 3 to 4 stems from red maple, northern red oak, sweet birch, and yellow-poplar, the most commonly occurring species on the site. The goal was to select stems so that seedling diameters up to 25.4 mm were as equally represented as possible. There were a limited number of seedlings from which to choose in smaller diameters, so in an effort to increase the sample size, diameters up to about 38.1 mm (1.5 in) were included. Five sweet birch were between 38.1 mm and 50.8 mm (2 in). Unlike complete or random sampling, this sampling methodology was uniquely designed to capture an equal representation of diameters, the variable of interest, and inferences about diameter distribution or densities cannot be made from this sample on the population. Experimental design in the larger existing study captures those data.

Post-burn seedling data was collected at the end of the 2014 growing season and included stem impact class (kill, topkill and sprout, no topkill), number of sprout stems per rootstock, dominant sprout diameter, height to the highest live bud, and if browsed, the number of sprout stems browsed per rootstalk.

Photographic documentation from various positions, angles, and heights was made throughout the data collection process to monument fuel loading, pre- and post-burn conditions, and fire effects on vegetation.

Prescribed Fire

The dormant season prescribed fire was conducted on April 18, 2014. Dormant season burns are conducted between leaf abscission in the autumn and the beginning of leaf expansion of the mesophytic hardwoods in the spring (Brose et al. 2013). Except for a few larger yellow-poplar and sweet birch seedlings just starting to exhibit signs, leaf expansion had not yet begun. Ignition operations on the lower burn unit started at approximately 12:55. Firing started from the control line on the east side of the unit with a backing fire downhill. Flanking fires were lit along the northern perimeter before firing the lower half of the unit. Total elapsed firing time was about 2 hours. Ignition operations in the upper burn unit were started at 16:00 the same day. The eastern control line was fired first with several parallel strip backfires before dot firing the down-slope western side of the unit. Total elapsed firing time was estimated to be 1 hour. During the burn window, temperature ranged from 19.5 to 22.0 °C (67.1 to 71.6 °F), humidity ranged from 22 to 28%, and wind speed ranged from 0 to 13.7 km/hr (0 to 5.8 mph). Weather data were obtained from Weather Station KVWPARSO3 in Parsons, WV, 5 km north of the study area.

Temperature measurements during the fire were recorded by 48 Hobo Type K data loggers connected to 25 cm (9.84 in) long probes with thermocouples placed on a square grid at the corners and center of the overstory plots, collocated at 48 of 50 seedling survival plots. Maximum temperature, duration, and heat index were calculated using the data from the synchronized data loggers. Heat index was defined by the cumulative temperature observations (Iverson et al. 2004), made at 3 second intervals, for the duration data logger temperatures were greater than 50 °C. Death of plant cells typically occurs at temperatures >50 to 55 °C (Waldrop and Goodrick 2012), so the heat index threshold was established accordingly.

Data Analysis

Analyses were conducted with SAS 9.4 statistical software (SAS Institute Inc., Cary, NC). When determining seedling response to fire, probability of survival was modeled by species using logistic regression. Herein, survival is defined as the probability that the rootstock of a topkilled seedling will produce at least 1 sprout that is alive at the end of the first growing season.

In preliminary analyses, all potentially explanatory factors were examined. These included species, pre-burn diameter, pre-burn height, “worst aggressor”, burn site (upper or lower), fence, and thermocouple temperature data. Temperature variables were defined by separate measures including duration, heat index >50 °C, and maximum temperature.

A logistic regression model optimized by species using Fisher’s scoring through backwards elimination was employed to determine if a species-specific probability of survival model including both diameter and height was superior to a model with only height or diameter, which was also modeled using logistic regression.

Probability of survival model is of the form:

$$P_s = \frac{e^{(\beta_0+\beta_1 X_1+\cdots+\beta_n X_n)}}{1+e^{(\beta_0+\beta_1 X_1+\cdots+\beta_n X_n)}}$$

Where:
P_s = species-specific seedling probability of survival
β_i = regression coefficients
X_i = independent variables used in the model

Significance of all models was evaluated at (α= 0.05). Model selection criteria included evaluation of the likelihood ratio test, parameter estimates, Akaike Information Criterion (AIC) values, and the Hosmer and Lemeshow Goodness-of-Fit test (H&L test). Non-significant values from the null hypothesis (β=0) likelihood ratio test precluded models from consideration, as did results from the H&L test that indicated the model did not fit the data. Models with all significant parameters and lower AIC values for models with the same number of parameters, were considered to be superior. The H&L test assesses whether the observed event frequency matches the expected event frequency in partition subgroup deciles of the model population (Moore et al. 2012). The null hypothesis is that the equation describes the data, and thus, models for which expected and observed event rates in subgroups are similar, are deemed well-calibrated. Corresponding p values >0.05 indicate models fit the data.

Pre- and post-burn height and diameter relationships by species were examined using linear regression to assess the degree to which pre-burn seedling stature can be used to explain the variability in first year post-burn growth. Distributions were not normal for 5 of 8 variables, but the lack of normality was improved with a square root transformation.

RESULTS

Pre-burn data

The goal was to obtain an equal diameter distribution of sizes to 38.1 mm (1.5 in), so effort was made for each stem selected to be measured to contribute to an equal representation of desired species sizes. While this was possible for yellow-poplar, fewer red oak was found in larger diameters, fewer sweet birch was found in smaller diameters, and red maple was not found in larger diameters.

A total of 692 stems were measured and tagged within the 50 seedling response plots in the burn units: 53 red maple, 236 red oak, 208 sweet birch, and 194 yellow-poplar (Figure 2 and Table 1).

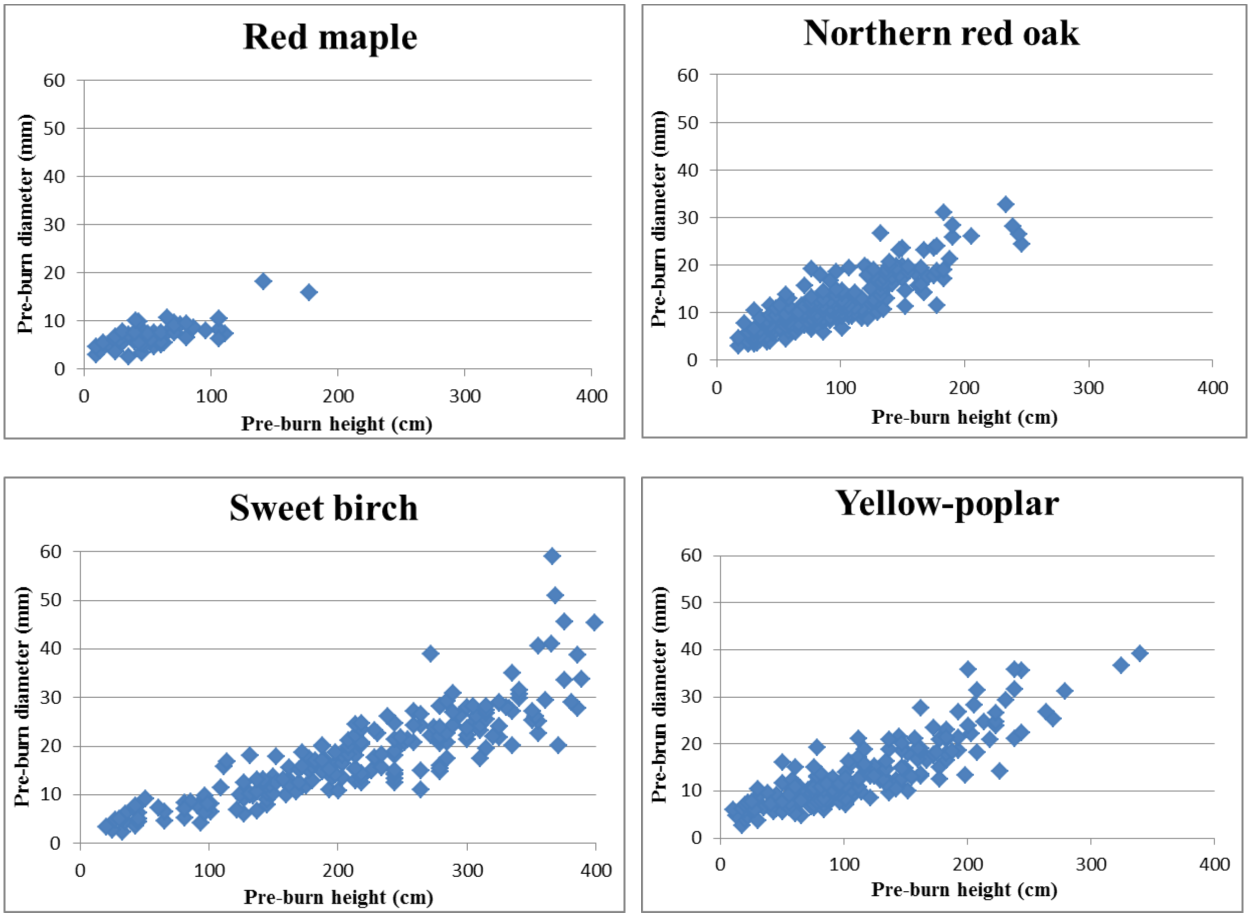

Figure 2. Pre-burn height and pre-burn diameter by species.

Table 1. Parameter estimates (standard error in parenthesis) for linear regression pre-burn height and pre-burn diameter models[a].

Species Model	Intercept	Height	R^2
Red maple	1.3938 (0.1745)	0.1649 (0.0232)	0.4979
Northern red oak	0.7743 (0.1085)	0.273398 (0.0111)	0.7199
Sweet birch	0.2305 (0.1466)*	0.2746 (0.0010)	0.7885
Yellow-poplar	1.0070 (0.1157)	0.2506 (0.0109)	0.7345

[a] Pre-burn size model is of the form: $D_s = \beta_0 + \beta_1 X_1$ Where: D_s = pre-burn diameter ($\sqrt{\text{mm}}$) of a seedling, β_1 = regression coefficients, X_1 = pre-burn height ($\sqrt{\text{cm}}$) of a seedling. * denotes parameter coefficient is not significant.

Tagged seedlings of all species were on average taller in fenced plots than non-fenced plots before the burn (Table 2).

Table 2. Pre-burn tagged seedling mean height in fenced and non-fenced plots.

	Mean height (cm)	
	Fenced	**Non-fenced**
Red maple	80	46
Northern red oak	106	81
Sweet birch	242	197
Yellow-poplar	126	101

Worst aggressor was recorded for each seedling tagged, with 520 of 691 seedlings having one or more aggressors. Arboreal aggressors were more common than non-arboreal aggressors. Representing 42%, the most common worst aggressor was sweet birch, 24% was blackberry (*Rubus* spp.), 10% was greenbrier (*Smilax* spp.), 5% was beech, 4% was striped maple (*Acer pensylvanicum*), 4% was red maple stump sprouts, and 3% was yellow-poplar stump sprouts. Various other species represented the remaining 8%.

Thermocouple data

Temperature data was captured by 48 thermocouples, 19 in the lower burn unit and 29 in the upper burn unit. The maximum temperature in the lower burn unit was 498.8 °C, the average maximum temperature was 171.0 °C, and the average duration >50 °C was 6.1 minutes. The maximum temperature in the upper burn unit was 498.8 °C, the average maximum temperature was 232.3 °C, and the average duration >50 °C was 6.4 minutes. Duration in minutes >50 °C and maximum temperature at each seedling survival plot with a thermocouple were mapped across the burn units (Figures 3 and 4).

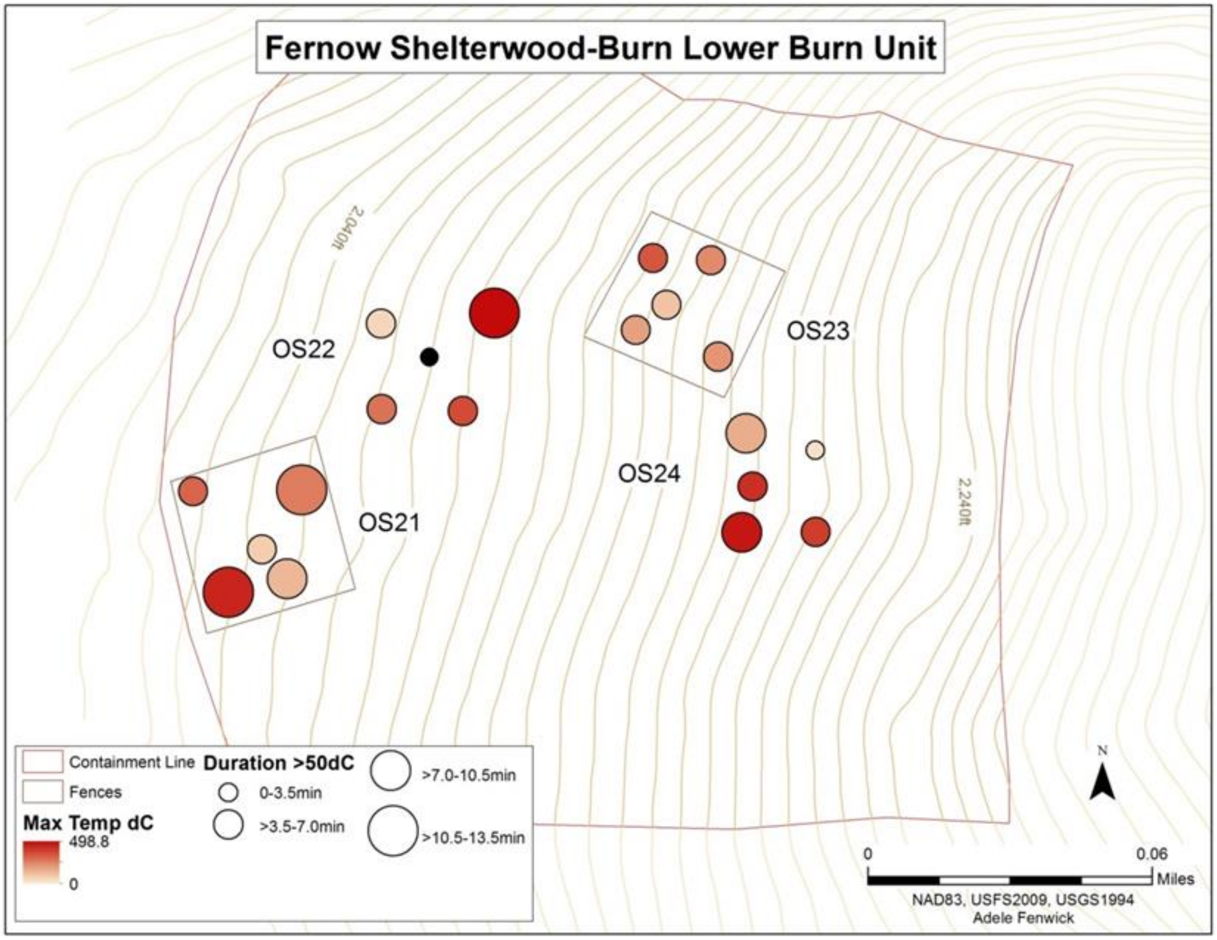

Figure 3. Lower burn unit thermocouple duration in minutes >50 °C and maximum temperature.

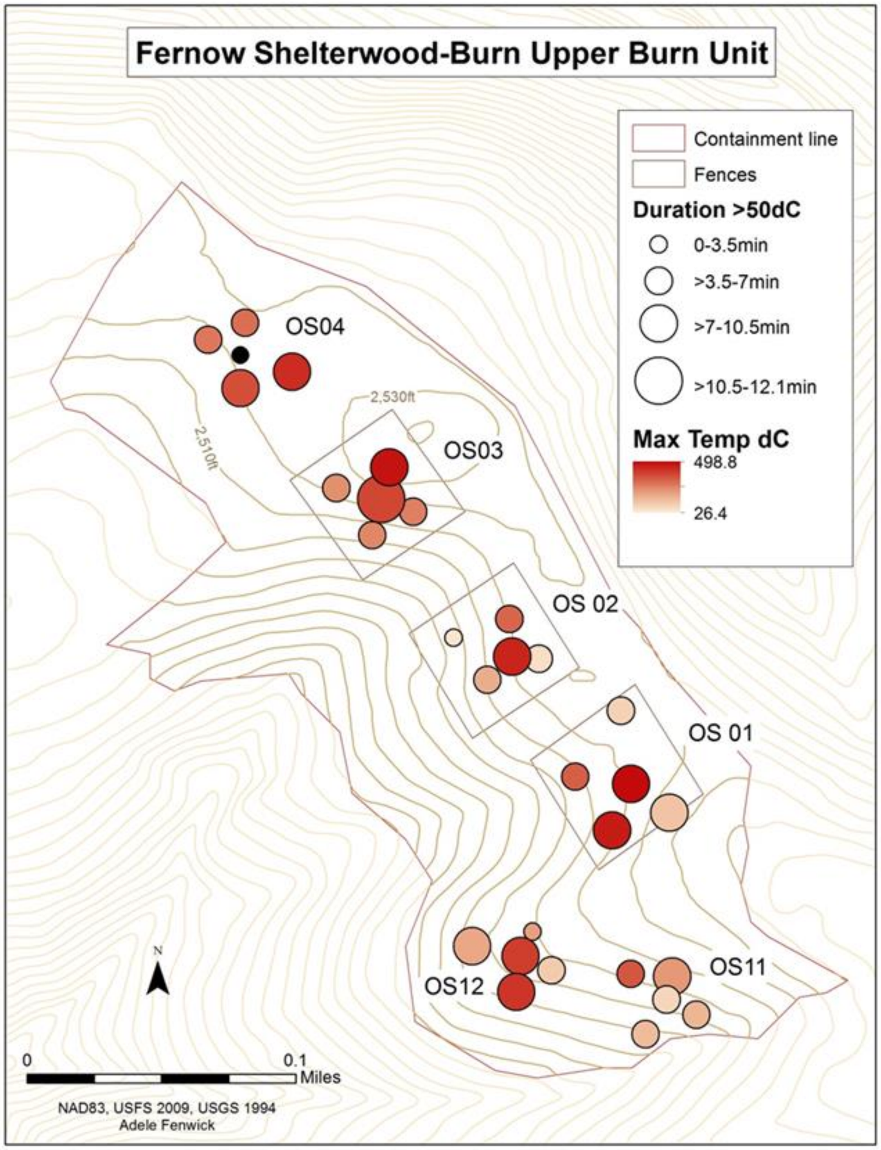

Figure 4. Upper burn unit thermocouple duration in minutes >50 °C and maximum temperature.

Post-burn data: Survival and growth

Survival

Of the 692 total stems tagged in the burn units, 691 were used in the data analysis. One seedling survived the fire without being topkilled and was excluded. Overall, 40% of red maple seedlings survived, 87% of red oak survived, 67% of sweet birch survived, and 48% of yellow-poplar survived.

At the end of the growing season post-burn, both red maple and red oak had an average of 2.1 sprouts per rootstock, sweet birch had an average of 3.4, and yellow-poplar had an average of 1.8.

At the end of the growing season post-burn, evidence of browse in unfenced plots was observed on 24 seedlings, of which 2 were red maple, 19 were red oak, 2 were sweet birch, and 1 was yellow-poplar. Although there appeared to be some differences between survival rates in the fenced and non-fenced plots, tagged seedlings of all species were taller in fenced plots pre-burn (Table 2). Meaningful conclusions related to the probability of survival could not be made with fence as an explanatory factor and survival probabilities are discussed independent of any potential effects related to the fence treatment.

Presence of a worst aggressor, maximum temperature, heat index >50 °C, and burn site (upper or lower) were not found to be significant factors during preliminary analyses in predicting survival and were not included in further analyses.

The model optimized by species using backwards elimination to predict probability of survival included both pre-burn height and diameter effects. Upon completion of removal steps optimized for red maple, the only significant effect to remain in the model was height. The null hypothesis ($\beta=0$) likelihood ratio was significant, as were both parameter estimates. The H&L

test indicated that the equation fit the data. Optimized for red oak, upon completion of steps, all effects were removed from the model. For sweet birch, only pre-burn height remained in the model and the likelihood ratio was significant, as were both parameter estimates, and the H&L test indicated that the equation fit the data. For yellow-poplar, both pre-burn height and pre-burn diameter remained in the model and the likelihood ratio was significant, however the H&L test indicated that the equation did not fit the data and consequently, did not meet model selection criteria. Reduced models by species using the main effect of pre-burn basal diameter and pre-burn height, separately, were also developed with logistic regression analyses. When modeling sweet-birch probability of survival using only diameter, the likelihood ratio and the H&L test were significant, but the intercept parameter coefficient was not significant. When modeling the yellow-poplar probability of survival using only diameter, the likelihood ratio, the H&L test, and all parameters coefficients were significant. Probability of survival using only diameter was not significant for red maple or red oak. Using pre-burn height only, probability of survival was significant for red maple, sweet birch, and yellow-poplar (Tables 3 and 4).

Table 3. Comparison and ranking of logistic regression probability of survival after one dormant season prescribed fire model[a].

Model	Red maple					Northern red oak				
	LR Pr >	I Pr>	V Pr >	AIC	H&L Pr>	LR Pr >	I Pr>	V Pr >	AIC	H&L Pr>
Height	0.0042	0.0043	0.0134	66.968	0.3867	0.1269	0.0025	0.1398	185.257	0.2638
Diameter	0.0741	0.0415	0.1014	71.985	0.9061	0.6132	0.0002	0.6181	187.332	0.8474
HD	-	-	-	-	-	-	-	-	-	-

Model	Sweet birch					Yellow-poplar				
	LR Pr >	I Pr>	V Pr >	AIC	H&L Pr>	LR Pr >	I Pr>	V Pr >	AIC	H&L Pr>
Height	<0.0001	0.0141	<0.0001	243.190	0.7622	<0.0001	<0.0001	<0.0001	253.091	0.2972
Diameter	0.0008	0.4052	0.0019	255.713	0.0743	0.0098	0.0124	0.0125	265.934	0.5214
HD	-	-	-	-	-	<0.0001	0.0135	<0.0001	-	0.0266

[a] Global null hypothesis (Beta=0) Likelihood Ratio Test (Pr>ChiSq) is indicated by: (LR Pr>). Model intercept parameter Pr>ChiSq is indicated by: (I Pr>). Size variable parameter Pr>ChiSq is indicated by: (V Pr>). Akaike Information Criterion is indicated by: (AIC). Hosmer and Lemeshow Goodness-of-fit test is indicated by: (H&L Pr>). Probability values >0.05 from the H&L test indicate the model fits the data.

Table 4. Logistic regression model[a] parameter estimates (standard error in parenthesis) for probability of survival after one dormant season prescribed fire as a function of height (cm) or diameter (mm).

Species Model	Height		Diameter	
	β_0	β_1	β_0	β_1
Red maple	-2.0490 (0.7180)	0.0285 (0.0115)	-1.7678 (0.8673)	0.1932 (0.1179)*
Northern red oak	1.2935 (0.4275)	0.0067 (0.0045)*	1.6809 (0.4534)	0.0179 (0.0359)*
Sweet birch	-0.9323 (0.3799)	0.0080 (0.0018)	-0.2854 (0.3428)*	0.0570 (0.0183)
Yellow-poplar	-1.2514 (0.3179)	0.0104 (0.0025)	-0.7955 (0.3180)	0.0531 (0.0212)

[a] Probability of survival model is of the form: $P_s = \frac{e^{(\beta_0+\beta_1 X_1)}}{1+e^{(\beta_0+\beta_1 X_1)}}$. Where: P_s = species-specific probability of seedling survival, β_i = regression coefficients, X_1 = independent variables diameter or height used in the model.
* denotes parameter coefficient is not significant.

Pursuant to the model selection criteria, the probability of survival as a function of height was the only model selected for consideration for red maple and sweet birch. The probability of survival model as a function of height and the model as a function of diameter were both considered for yellow-poplar, but the model as a function of pre-burn height had a lower AIC value and thus, was considered superior. Survival of red oak regeneration was so high that a meaningful logistic regression model could not be derived with any significant effects (Figures 5 and 6).

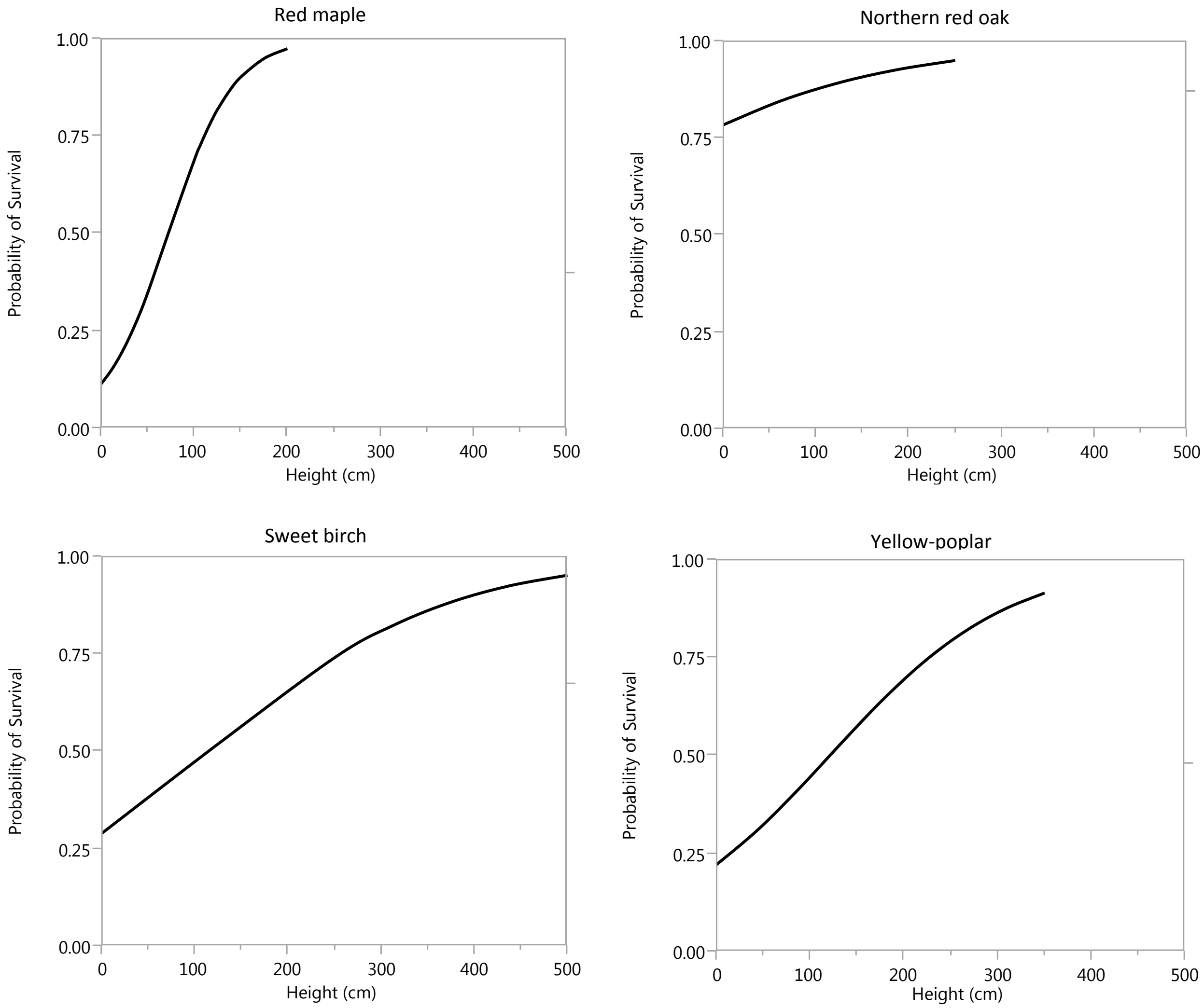

Figure 5. Probability of survival by species as a function of pre-burn height.

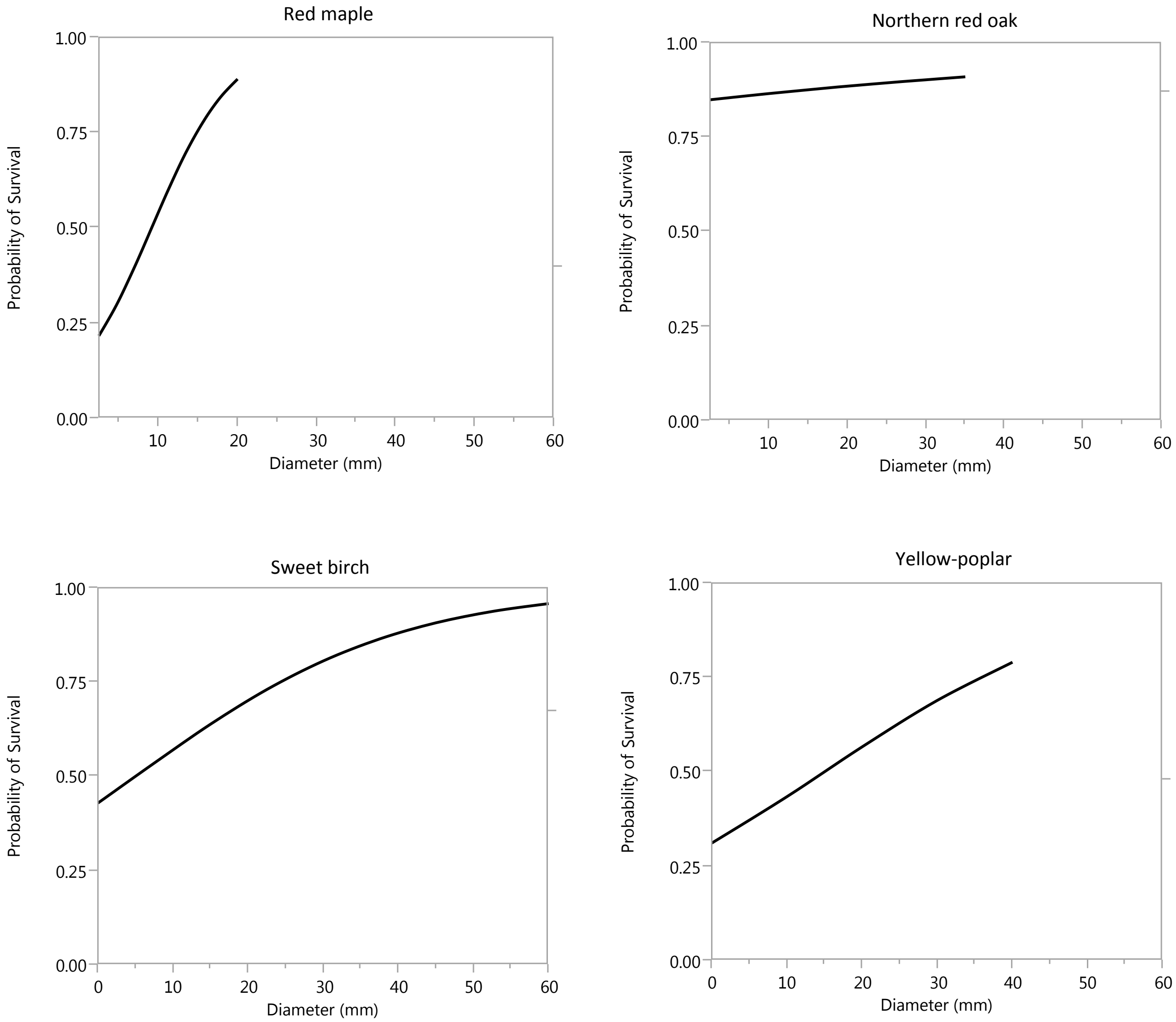

Figure 6. Probability of survival by species as a function of pre-burn diameter.

Growth

Linear regression analysis of pre- and post-burn height and pre- and post-burn diameter by species examined the extent to which pre-burn size could explain post-burn size variability at the end of the first growing season. Values were square root transformed because data were not normally distributed. For red maple and red oak, there was a stronger relationship between pre-burn diameter and post-burn height growth than pre-burn height and post-burn height. For sweet birch and yellow-poplar, more about post-burn height variability was explained by pre-burn height than pre-burn diameter (Figures 7, 8 and 9, and Table 5).

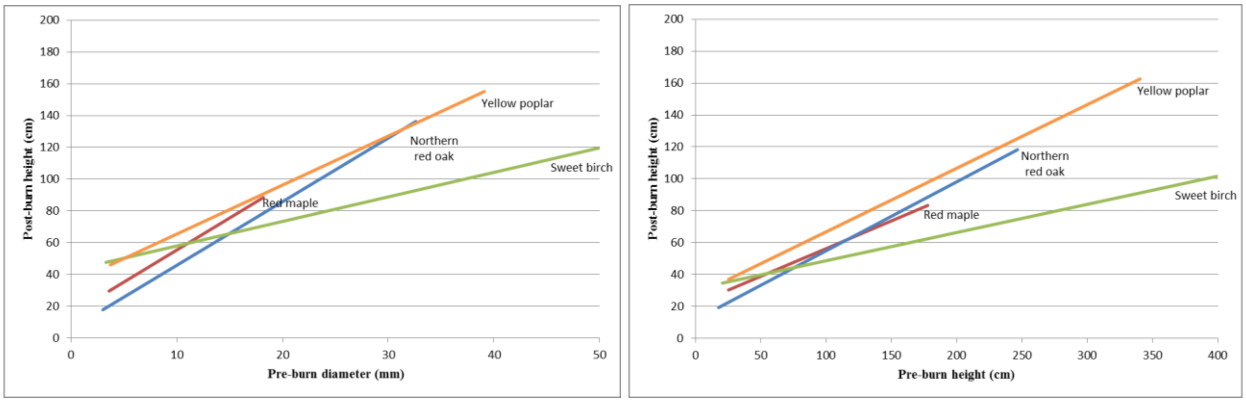

Figure 7. Linear regression of post-burn height and pre-burn height and diameter by species.

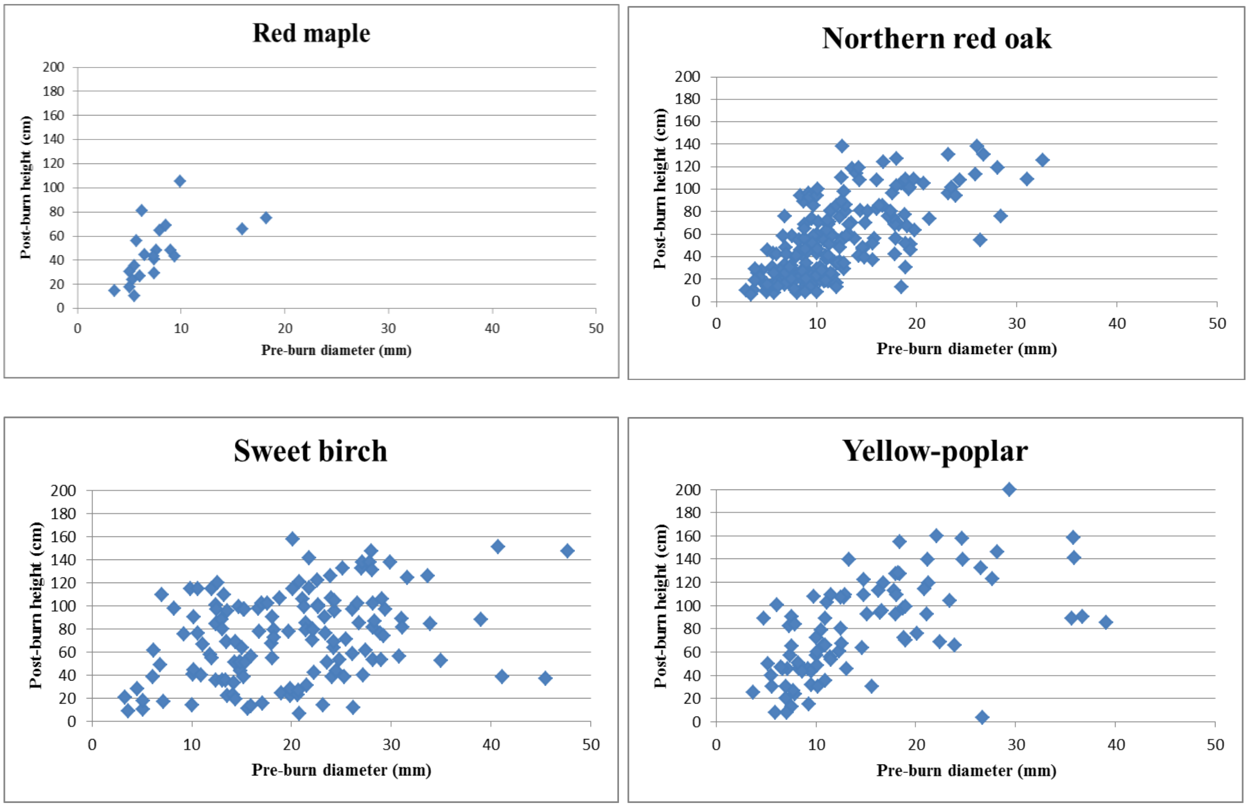

Figure 8. Relationship between the pre-burn diameter and first year post-burn height growth by species.

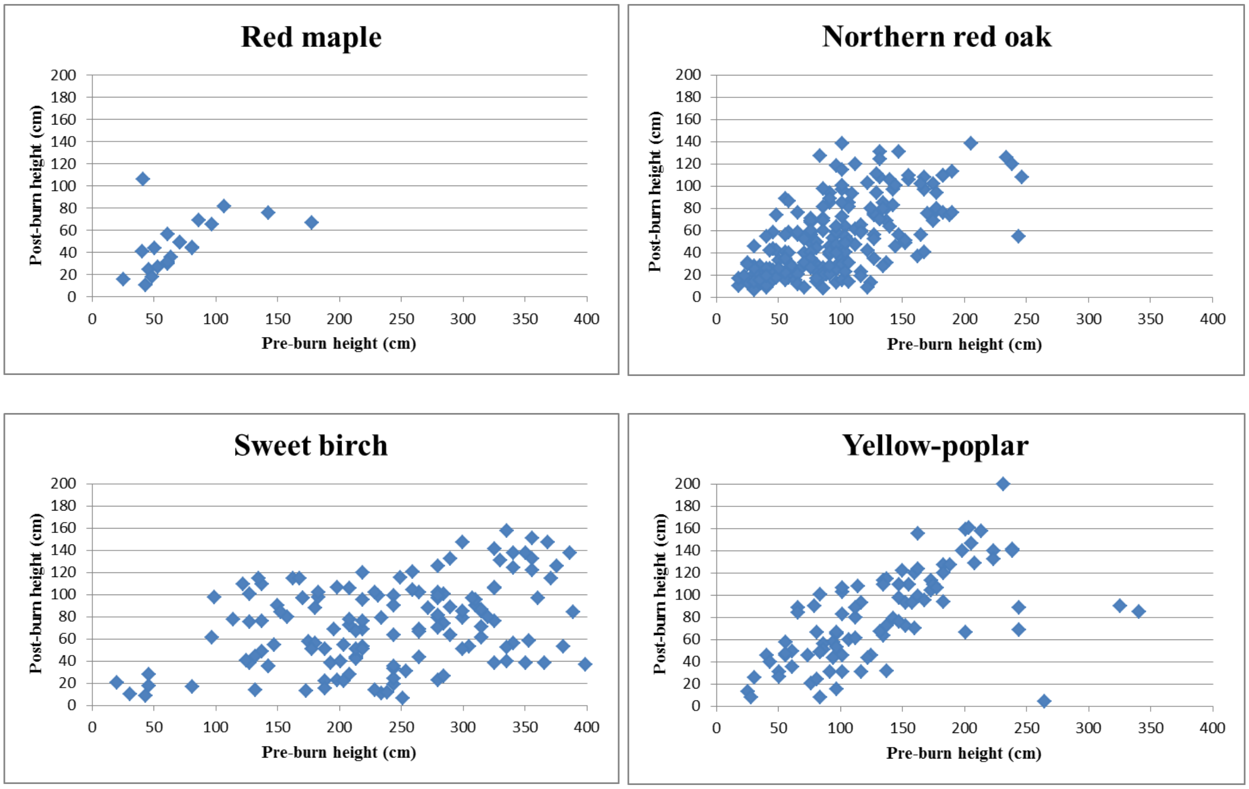

Figure 9. Relationship between the pre-burn height and first year post-burn height growth by species.

Table 5. Model^a parameter estimates (standard error in parenthesis) of first year height growth following one dormant season prescribed fire as a function of height or diameter.

Species Model	Pre-burn Height			Pre-burn Diameter		
	β_0	β_1	R^2	β_0	β_1	R^2
Red maple	*2.1364 (1.4652)	0.5379 (0.1729)	0.3376	*0.9750 (1.5696)	2.0533 (0.5637)	0.4112
Northern red oak	1.2777 (0.5166)	0.5938 (0.0526)	0.3859	*0.1048 (0.5284)	2.0298 (0.1531)	0.4641
Sweet birch	3.3445 (0.9308)	0.3218 (0.0599)	0.1723	4.3842 (0.8409)	0.8804 (0.1873)	0.1379
Yellow-poplar	2.2823 (0.8485)	0.5629 (0.0732)	0.3942	3.0536 (0.8141)	1.4946 (0.2111)	0.3551

[a] First year post-burn height growth models are of the form: $H_s = \beta_0 + \beta_1 X_1$ Where: H_s = height ($\sqrt{\text{cm}}$) of a seedling at the end of the first growing season, β_i = regression coefficients, X_1 = independent variables pre-burn diameter ($\sqrt{\text{mm}}$) or pre-burn height ($\sqrt{\text{cm}}$) used in the model. * denotes parameter coefficient is not significant.

DISCUSSION

The two previous seedbed preparation burns in earlier stages of this study were effective in reducing the maple component of the stand. Prior to burning in 2002/2003 and 2005, maple had been most abundant, but after burning twice, maple, oak, and yellow-poplar were approximately equally represented, however, sweet birch was the most abundant (Schuler, T.M. et al. 2013). The reduction in red maple was apparent in the difficulty finding sufficient numbers of red maple seedlings, particularly in the larger diameters, to tag for the study. Thus, it is hard to make any meaningful probability of survival conclusions about red maple, especially at larger diameters and heights. The increased abundance of sweet birch was reflected in the "worst aggressor" assessment, representing 42%. Although there was not an overall shortage of sweet birch stems, very few were located that represented smaller diameters, illustrating their rapid growth.

Brose et al. (2006) review of species sensitivity levels to fire was generally consistent with the results presented here. Northern red oak is considered to be resistant to fire, which was confirmed by its overall 87% survival rate. As a seedling, yellow-poplar is considered to be very sensitive to fire which was confirmed in this study by an overall 48% survival rate. Brose and Van Lear (1998) reported approximately 29% yellow-poplar survival in a dormant season shelterwood-burn in Virginia that was also conducted 4 years after a seed cut. Sweet birch is considered fire-sensitive, which is somewhat supported by a 67% survival rate. Ward and Brose (2004) reported about 24% of birch survived a burn following the final removal cut in Connecticut. Red maple is considered to be fire-sensitive to intermediate, depending on fire intensity, seasonality, and seedling size (Brose et al. 2006, Ward and Brose 2004). Only 53 red maples in the desired size classes were located and most of them were less than 12.7 mm (0.5 in) and 60.96 cm (2 ft) tall. About 40% of the red maple survived, illustrating their sensitivity at small sizes. Unfortunately, the small stature and size of the sample discourages making conclusions about larger red maple seedlings based on these results. Brose and Van Lear (1998) reported 64% survival for red maple following the aforementioned dormant season shelterwood-burn in Virginia, and Ward and Brose (2004) reported between 55% and 90% survival in Connecticut.

Greater differences in mortality among species are frequently reported in the small seedling size classes (Kruger and Reich 1997, Brose and Van Lear 1998, Brose and Van Lear 2004). This is especially apparent when comparing oak to red maple, sweet birch, and yellow-poplar in this study. The probability of survival for oak is reported to increase with increasing diameter (Brose and Van Lear 1998, Dey and Hartman 2005); however, for the range of seedling sizes examined in this study, probability of survival slightly increased with size, but was not statistically significant. Results indicate that although diameter was a significant variable for predicting survival for yellow-poplar, height was a better predictor with a lower AIC value and a lower null likelihood ratio statistic. The growth strategy of greater aboveground than belowground biomass allocation of red maple, sweet birch, and yellow-poplar is probably related to why the probability of survival as a function of height is a superior model. The significance of height or diameter in predicting survival may change following future growing seasons if there is a bias in height or diameter of future mortality (Sander 1972). This is one of several reasons to proceed with caution when interpreting the effects of prescribed fire using only first year results.

Carbohydrate allocation to the taproot provides reserves that are necessary for repeated sprouting, but this is hard to quantitatively assess without excavation. A small stem may be a seedling or a seedling sprout that has experienced episodes of dieback and sprouting (Johnson et al. 2009). Thus, stem size is not always indicative of age or root system size and consequently, stem size does not always reflect the capacity to sprout. Some studies have shown that young oak seedlings can suffer high mortality after a low intensity dormant season burn under the shade of a mature stand (Johnson 1974, Wendel and Smith 1986). The increase in fire induced mortality they saw is likely in large part attributable to the difference in root carbohydrate reserves of seedlings growing in shade under a full canopy compared to seedlings of the same size growing in more open environments (Brose et al. 2013, Wendel and Smith 1986). Part of the reason that even small oaks were able to consistently sprout in this study was likely the root:shoot ratio development of those seedlings surviving two seedbed prep burns, as well as the ratio developed by the seedlings that germinated after the 2005 spring burn and 2005 bumper acorn crop (Schuler, T.M. et al. 2013). This new cohort of seedlings was able to respond to the increased light environment following the seed cut and replenish carbohydrate reserves. The ideal choreography in timing the burn before a bumper acorn crop is evident following those events.

Survival probabilities are important to examine in conjunction with the “re-growth”, or height of resprouted stems (Brose 2004), to assess the future competitiveness of the oak advance reproduction in anticipation of the final removal cut. Height growth of new sprouts from advance reproduction is related to the size of the stem prior to damage, degree of shading, and site quality (Belair et al. 2014, Brose et al. 2013). Perhaps attributable to oak’s conservative growth strategy of greater root than shoot biomass allocation, and the larger root:shoot ratio that they develop (Barnes and Van Lear 1998, Johnson et al. 2009), the larger the pre-disturbance stem size, the faster the new sprout will grow (Sander 1971, 1972). First year growing season data indicated that the relationship between pre-burn diameter and post-burn height in red oak is the strongest of all pre- and post-burn heights or diameters among species. Not surprisingly, much more of red oak first year post-burn height growth variability can be explained by pre-burn diameter than pre-burn height. More variability about red maple post-burn height can be explained by pre-burn diameter than pre-burn height, but the relationship is weaker than that in oak. This is in contrast to pre-burn height explaining more about post-burn sweet birch and yellow-poplar height growth. Similar to the superiority of height as a predictor of survival for sweet birch and yellow-poplar, a stronger pre- and post-burn height relationship may be attributable to their exploitative growth strategy of greater shoot than root biomass allocation.

Northern red oak shoot growth is episodic. When moisture, light, and temperature conditions are amiable, multiple shoot growth flushes followed by rest periods, during which most roots elongate, will occur in the same growing season (Reich et al. 1980). In contrast, under undisturbed canopies growth is slow and generally limited to one flush (Sander 1990). More than one flush was visible on numerous seedlings in the burn units. Roots were not examined but the post-fire conditions that facilitated multiple flushes may have also provided for significant root elongation and growth. This is especially important for the survival of smaller oak seedlings that may not have had large root systems and carbohydrate reserves pre-burn, and may struggle to survive past the first growing season.

In addition to the probability of survival increasing with stem height, post-burn height growth increases with pre-burn stem height for sweet birch and yellow-poplar. This illustrates that the capacity to control oak competitors may be reduced as the duration between the seed cut and the release burn increases. These results indicate that red oak appears to exhibit a consistent ability to survive regardless of diameter, but it is questionable that the smaller diameter oaks will produce a sprout that will grow fast enough to compete successfully with other species, particularly yellow-poplar and sweet birch survivors, and become at least codominant in the stand (Sander 1971). Although referring to post-harvest sprouting, not post-burn sprouting, Sander (1971) speculated that stems of oak advance reproduction must be at least 12.7 mm (0.5 in) in diameter before it will produce a new sprout that will grow fast enough to compete successfully. Brose et al. (2014) indicate that although oak seedlings with root collar diameters greater than 6.40 mm (0.25 in) will likely sprout, it is recommended not to burn until oaks are at least 12.7 mm (0.50 in) in diameter and 30.48 cm (1.0 ft) tall. Moreover, oaks with root collar diameters greater than 19.1 mm (0.75 in), with sufficient light levels, are capable of relatively rapid, sustained height growth (Brose et al. 2014). When assessing advanced regeneration in anticipation of a cut, “competitive oak” seedlings taller than 91.44 cm (3 ft) with root collar diameters greater than 19.1 mm (0.75 in) are highly likely to be at least codominant at crown closure following overstory harvest (Brose et al. 2008). In this study, results from the first growing season growth indicate a similar pre-burn diameter is necessary for oaks to be a competitive height after the first year. For example, using the pre-burn diameter and post-burn height equation developed from the data for oak (Figure 2 and Table 1), to reach a comparable height as the average tagged yellow-poplar of 80.54 cm (2.64 ft) following the first post-burn growing season, a red oak would have to be 19.1 mm (0.75 in) at the time of the burn. This is the same as Brose et al. (2014) size threshold guidelines that suggest oak seedlings need to be at least 19.1 mm (0.75 in) at the time of the burn to be capable of rapid height growth.

Although 52% of yellow-poplar seedlings did not survive, survivor height growth was rapid. Reducing the height discrepancy between yellow-poplar, sweet birch, and oak is important in the short-term and, even if only temporarily, allows increased oak height growth and root development (Ward and Brose 2004). Ultimately, reducing the density of those competitors is also necessary. Yellow-poplar will out compete oak even when they are both free-to-grow at crown closure, and it is only where yellow-poplar is excluded at crown closure on good sites that oaks will be successful (Loftis 2004).

Although the managerial intent is not to create an oak monoculture (Smith, H.C. 1993), in the absence of additional disturbances the remaining sweet birch and yellow-poplar may continue to out compete oak, eventually forming a closed canopy and displacing oak. However, a concern with additional competition control measures, specifically fire, would be that although burning again may further reduce competitor stem densities, it may also jeopardize the recruitment of the oak seedlings into larger sizes (Schuler, J.L. et al. 2013). Burning after the final removal cut is a lesser studied, but potentially effective competition control method (Brose 2013).

In earlier stages of this study, the influence of the seedbed preparation burns was apparent in the correlation between the post-fire conditions and enhanced red oak establishment. The timing of the 2005 burn before an abundant acorn crop was ideal, and density in 2006 was almost 10,000 oak seedling/ac of all sizes. Before the 2 seedbed prep burns there were about 50 larger oak seedlings/ac, but by 2009 the density of large oak seedlings was over 1,500 stems/ac. In contrast, there were almost no larger oak seedlings in the unburned control plots in the previous 10 years (Schuler, T.M. et al. 2013). Although fire helps improve the seedbed to facilitate successful oak germination and seedling establishment, it can also create favorable conditions for other species to germinate which may translate to an overall unchanged relative abundance of oak (Brose et al. 2013). Reports of increased yellow-poplar seedling abundance post-burn are not uncommon, and sweet birch has also been particularly problematic (Barnes and Van Lear 1998, Shearin et al. 1972, Schuler et al. 2010). Following the two seedbed prep burns in 2002/2003 and 2005, sweet birch and yellow-poplar seedlings increased tenfold by 2006 (Schuler, T.M. et al. 2013). The seedbank was sampled prior to and after the fire in 2005 and sweet birch and yellow-poplar were 2 of 5 species comprising 76% of the post-burn seedbed (Schuler et al. 2010). Enough seedlings survived or germinated following those burns and grew sufficiently for sweet birch to represent 42% of the "worst aggressor" population in 2014. Hence, fire can have unintended, although not unexpected, problematic effects. This challenge is not unique to disturbances following fire; yellow-poplar and sweet birch seedlings can have the highest importance of tallest stems and express canopy dominance in the high-light environment of young stands following clearcutting (Brashears et al. 2004, Sander and Clark 1971). Stemming from prodigious seed production, seedbank accumulation, and rapid early height growth, controlling these species proves to be a significant management challenge faced on mesic sites.

The type and location of seeds, and their chemical and thermal seed dormancy and seedbank longevity likely determines whether they will persist as a species in a regime of frequent fire (Dey and Fan 2009). Repeated landscape-level burning by Native Americans and settlers may have altered seedbank dynamics (Schuler et al. 2010) by suppressing overstory competition from fire-sensitive species whose seeds have carry-over capacity, thereby reducing seedbank contribution, as well as decreasing the seedbank storage from reduced viability following repeated fire. Compared to more xeric sites, the extant arboreal seedbank may present additional resistance to oak restoration efforts on mesic sites (Schuler et al. 2010, Schuler and Liechty 2008). Although this was the third fire in 12 years in the treatment area, it was the first fire in the post-seed cut young stand. Inventory in future years will indicate if favorable conditions for additional oak competitors to germinate from the seedbank were created by the combination of the high-light environment following the seed cut in 2009-2010 and the burn in 2014. One fire seldom causes long-term shifts in species composition (Van Lear 1991, Van Lear and Watt 1993), so further efforts may be necessary to reduce the amount of sweet birch and yellow-poplar seedlings and seedbank.

Blackberry was the second most common pre-burn “worst aggressor” with 24%. This figure does not reflect its ubiquitous presence in the plots however. Sweet birch only represents a larger proportion of the “worst aggressors” because it was usually the tallest of the competing vegetation, not because it was the most frequently occurring competitor. Schuler et al. (2010) found that in addition to yellow-poplar and sweet birch, blackberry was one of the 5 species that comprised 76% of the post-burn seedbank in 2005. They found no evidence that blackberry abundance was affected by prescribed burning because it became the most abundant species in the seedbank, at the expense of decreased abundance of other species. Although not quantitatively measured, qualitative observation during data collection following the 2014 burn confirms blackberry to be unaffected by fire. In particularly thick areas of blackberry canes, visibility of the forest floor was inhibited by the foliage and dense shade was cast. The degree to which blackberry thickets potentially affected the survival and growth of seedlings is not known (Donoso and Nyland 2006), but it would likely be more detrimental to yellow-poplar and sweet birch. Yellow-poplar growth could be inhibited by the shade and the lower root:shoot ratios of sweet birch and yellow-poplar may have been exhausted to a greater degree than oak. Oak may be negatively impacted by blackberry thickets, but perhaps not to such a degree as other species. Similar to persistence exhibited in response to the seemingly destructive effects fire, blackberry may bestow a benefit to oak only manifest by the detriment to yellow-poplar and sweet birch.

Fire characteristics influence the degree to which shoot and root tissues are exposed to lethal temperatures, and the ability of a seedling to withstand these effects and survive is differentiated by species and the degree to which tissues are protected by bark or soil (Waldrop and Goodrick 2012). Acknowledging the discrepancies between temperature measurement devices used in different studies (Bova and Dickinson 2008), thermocouple temperatures observed in the 2014 Fernow burn were within the general range observed elsewhere including: Dey and Hartman (2005) in the Missouri Ozarks recorded 121 to 316 °C, Iverson and Hutchinson (2002) in Ohio recorded 163 to 316 °C, Iverson et al. (2008) between 2 fires in Ohio recorded 140 to 211 °C, Iverson et al. (2004) in Ohio recorded 129 to 427 ° C, Greenberg et al. (2012) in South Carolina recorded <79 to <371 °C, and Alexander et al. (2008) in Kentucky recorded 148 to 583.5 °C.

Following several years of monitoring, delayed mortality differences between species have been observed (Yaussy and Waldrop 2010), indicating that the percent of surviving seedlings may decline at different rates. Yaussy and Waldrop (2010) found that peak fire temperature caused greater delayed mortality than duration of exposure over a 4 year period, so perhaps a relationship between fire intensity and seedling survival will be revealed in time. In addition to delayed mortality differences on a species gradient, delayed mortality can also differ on a size gradient (Sander 1972). The small oak stems < 6.4 mm (0.25 in) showed a strong ability to survive the burn, but their persistence over the next several years will indicate if their survival was just a short-term phenomenon. Furthermore, height growth is frequently not linear during the first years following treatment, and even a relatively light residual overstory reduces growth of all reproduction (Sander 1972). By design, shade from the residual overstory trees will likely slow growth rates or induce mortality to a greater degree for more light-demanding species. As gaps created by the seed cut close and the short-lived gap-filling species decline, differences in survival and importance value may emerge (Thomas-Van Gundy et al. 2014). It appears that a successful regeneration will in part hinge on the degree sweet birch and yellow-poplar are affected.

There is cause to pause when interpreting these results, as first year growth is a tentative assessment and dynamics may change meaningfully over time. Delayed mortality and growth rate dynamics, as a function of species, size, and perhaps fire characteristics, may change in coming years and more definitive conclusions can be made about how the shelterwood-burn sequence affected the competitive position of oak. Brose (2010) presented promising results in a follow-up to an early shelterwood-burn study (Brose and Van Lear 1998) that show the increased density of oak stems and decreased red maple and yellow-poplar stems found 2 years post-fire, persisted after 11 years. Additionally, the number of dominant oak increased with fire intensity, while the number of red maple and yellow-poplar dominant stems decreased (Brose 2010).

CONCLUSION

The historical record throughout much of the central hardwood region indicates fire created and maintained the conditions necessary for sustaining oaks where they may not have otherwise occurred, and it is doubtful that oaks on mesic sites represent a true self-perpetuating climax in the absence of fire (Abrams 1992, Lorimer 1993, Schuler and McClain 2003). The intersection of many fortuitous events that led to oak expansion and dominance likely cannot be recreated with singular or uniform silvicultural methods. Oak forests have historically been maintained as uneven-aged communities by periodic canopy disturbance and surface fires, or as even-aged communities through stand-replacing events. In the early 20th century oak canopy recruitment occurring even in the absence of major disturbances, and the ability of oak to compete following old-growth logging represent two models of oak recruitment and response to disturbance that the lack of fire has functionally changed (Schuler and Fajvan 1999). Historical disturbance pathways are being displaced by new and different successional processes that create transitional oak communities, which eventually convert and exclude oak altogether (Brose and Waldrop 2010). The ability of oak to survive in the understory until release is contingent on understory light levels and the competitive environment. These two factors explain the biggest difference between the past and present condition of stands and the ability to maintain a dominant oak component in the canopy (Rentch et al. 2003).

The composition and structure of many mesic and xeric sites has assumed an unperturbed disposition in absence of fire, which may explain why oak species have trouble competing on a range of sites. Temporary conversion of mesic sites to xeric conditions by a long regime of low intensity fires, or several intense fires, may have resulted in the ability of oaks to dominate sites where more mesic species normally occur (Van Lear 1991). On drier sites where fire was more common, mesic species are now able to occupy some of the locations that were previously unsuitable, or on the fringe of their tolerance level, further displacing oak. Examples include yellow-poplar stands reaching ridgetops and rhododendron extensively increasing its extent (Van Lear and Waldrop 1989). Even the species that are fire-sensitive have grown to sufficient sizes to now resist fire damage or mortality, such as yellow-poplar and red maple (Van Lear 1991).

There is tremendous spatial variability in historical fire regimes and information from cultural and biological studies help elucidate the relationship between fire and oak community dynamics (Schuler and McClain 2003). Valuable biological record contributions to fire regime research include paleoecological, dendrochronological, and dendroecological examinations, which may examine charcoal from sediment or soil cores, and cross-section fire scars (Guyette et al. 2011, Hart and Buchanan 2012, Patterson 2006). Sophisticated data-driven spatial models that incorporate historical fire frequency, vegetation and climatic factors, and site-species relationships have also been developed (Guyette et al. 2012, Thomas-Van Gundy et al. 2007 Thomas-Van Gundy and Strager 2012). These records and models identify areas that may be suitable for silvicultural treatments to maintain or restore oak competitiveness, or to mimic historical disturbance regimes.

It is clear that there is not a singular or uniform solution to oak regeneration and recruitment challenges. Location characteristics and species composition variability preclude a uniform silvicultural method. Studies have shown that cutting or fire alone will frequently not be sufficient (Moser et al. 1996, Schuler and Miller 1995). Fire is a blunt tool and in many instances may serve as only part of the solution that also includes more precise methods. Treatment components will likely include a combination of some or all of the techniques with demonstrated efficacy, including herbicide, various precommercial and commercial harvests, deer exclusion, crop tree release, and fire (Arthur et al. 2012, Brose 2010, Brose et al. 2008, Miller 2000, Thomas-Van Gundy et al. 2014).

The 3 models developed from the pre-burn and first year post-burn data were designed to be used singularly or in conjunction with each other when developing silvicultural prescriptions. The pre-burn height-diameter relationships may be useful for estimating diameters if only heights are collected in an inventory, and the pre-burn and post-burn size relationships can help predict first year growth of the seedlings that are expected to survive according to the probability of survival models. Successful oak regeneration is related to the size and number of advanced seedlings present when harvests occur (Loftis 1990b, Sander and Clark 1971). Loftis (1990a) provided dominance probabilities as a function of size, indicating that as seedling size and probability of survival increase, fewer seedlings are needed to ensure sufficient regeneration following harvest. Prescribed fire seedling survival and growth models serve as a complement to dominance probabilities for short- and longer-term stand projections. To contribute effectively to the body of knowledge created from a unified monitoring approach, prescribed fire seedling response models are necessary for a wide range of stand conditions and species mixes, and include the fire characteristics and underlying stand history.

The models developed from this study are a function of characteristics and interactions that are specific to these stands. They serve as a reference but their site-specific nature may limit them to stands with similar attributes, precluding direct applicability elsewhere, and illustrate the importance of replications examining fire effects across different landscapes. First year results serve as the point from which changes will be measured, and usefulness of the models will continue to materialize as the stand develops and the future competitiveness of the oak component becomes more clear. Monitoring how the stand develops in the coming years will help contribute to knowledge about effects of the shelterwood-burn method in mesic mixed-oak stands on good sites (SI 70) in the central Appalachian Mountains. Unarguably, more long-term data and studies are needed. With the ability to predict outcomes of seedbed preparation and release burns more reliably, prescription development will be more easily navigable.

Restoring functional oak ecosystems includes complex issues beyond simply the direct effect on oak regeneration. It is important to consider other ecosystem attributes including potential positive and negative impacts on the seedbank, sensitive flora and fauna, watersheds, soils and obligate soil biota, the nutrient cycle, insect populations, and wildlife habitat. Many species of wildlife developed to depend on fire-maintained conditions, and as the role of fire has declined, so have many wildlife species (McShea and Healy 2002). From an economic perspective, a prescription including prescribed fire must be compatible with timber production (Marschall et al. 2014, Wiedenbeck and Schuler 2014). Other concerns and management constraints that may influence the use of prescribed fire include liability issues in the wildland urban interface, local burn policies, cost, landowner objectives, air quality impacts, and availability of qualified fire management personnel (Cleaves et al. 1999).

Many silvicultural methods are necessary to shape the “regeneration niches”, expressed by events and associated ecological conditions which favor oak and widen their regeneration window (Johnson et al. 2009). Immense effort has been made in analyses and literature reviews to identify common denominators in success and failure to promote oak using fire (Brose et al. 2006, Brose et al. 2013, Brose et al. 2014), and continued research will contribute to refining techniques and validating in which situations fire can be a beneficial component of silvicultural methods to maintain or restore oak communities. The requirements of forest management in diverse eastern ecosystems require adaptive methods and further research to support decisions that address complex problems (Nowak et al. 1997).

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